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Evolution of the biosphere

Symptoms of Ecological Crises

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Manuscript received January 26, 1993

Abstract – A list of ecological crisis symptoms, empirically observed from the paleontological record and reconstructed, is presented. The symptoms are founded in the results of a study of the global crisis of continental biocenoses in the mid-Cretaceous time and of the largest paleontologically documented crisis in the assemblage of the terrestrial tetrapods in the Early-Middle Jurassic.

We live in an epoch of a progressively evolving anthropo-stimulated ecological crisis, which threatens not only the Earth's biosphere but civilization as well. The single experience that humanity has at its disposal is that of history (Blok, 1986). Therefore, the reconstructions of the biosphere history on the basis of the geological record and, in particular, the study of the preconditions, natures, and consequences of the ecological crises of the Earth's geological past play an important role (Sokolov, 1983, 1988). Based on that knowledge, we can predict the character of the negative consequences of recent crises and can elaborate an adequate strategy of behavior in the conditions of its progressive development.

Furthermore, already obtained results, mainly in the Paleontological Institute of the Russian Academy of Sciences, testify unequivocally that the crisis epochs are of short duration only in the geological time scale. As to "the ripening" of the preconditions of the ecological crises and their relaxation, these processes prove to be even geologically long. Therefore, referring to geological history seems to be an absolute necessity in correctly estimating the scale of the duration of the crisis with which humanity has collided. The research of the ecological crises of the rather distant past, although only indirectly acquainted with their long-term consequences, acquires, therefore, a particular role.

The formulation of the symptoms of the ecological crises is an important step in that direction. The symptoms are essentially a syndrome (Fedonkin, 1991), which expresses, in a very general form, the regularities of the crisis processes in the Earth's biosphere. The following list of symptoms summarizes the results of two large ecological crises with different characteristics from the geological past.

The first of them is the global crisis of the land and freshwater basin biocenoses in the mid-Cretaceous time, studied in the Laboratory of Arthropods of the Paleontological Institute of the Russian Academy of Sciences (Rasnitsyn, 1972, 1988, 1989, 1990; Zherikhin and Sukacheva, 1973; Kalugina, 1974, 1977; Rodendorf and Zherikhin, 1974; Kalugina and Zherikhin, 1975; Zherikhin, 1978, 1979, 1980, 1987; Zherikhin and Kalugina, 1980; Zherikhin and Rasnitsyn, 1980; Dmitriev and Zherikhin, 1988). This crisis was studied most carefully from the fossil insect records, but participation of other components of the biota were revealed as well: higher plants (Meyen, 1987; Vakhrameev, 1988), some other groups of terrestrial invertebrates (bivalves, gastropods, ostracods, chelicerats, and others), and vertebrates (fishes, amphibians, reptiles, birds, and mammals). For insects and higher plants at least, this crisis was the largest in the history of the biosphere. Vertebrates reacted to it considerably less strongly (Kalandadze and Rautian, 1983, 1993a). Data on this crisis allowed V.V. Zherikhin to formulate the concept of the biocenotic regulation of phylogenesis. The main attention in this concept is given to the regulatory influence of the structure of the adaptive zones and ecological niches of the shaped biocenosis, historically formed in the course of a long phylogenesis (Vakhrushev, 1988) and constantly reproduced (Rautian, 1993), on the processes of the phylogenesis of taxa, which are the constituents of a biota. According to this concept, the disruption of the structure of the biocenosis provokes an ecological crisis. This idea can be considered an important step in the formulation of the theory of the evolution of biocenoses (and not only of the reconstruction of the particular phylogeneses). The absence and necessity of such a theory have been emphasized by many authors (Zavadskii, 1968; Timofeev-Resovskii *et al.*, 1969; Duvin'e, 1979; Shvarts, 1980; Kolchinskii, 1990; Margalef, 1992).

The second crisis was discovered and studied by us (Kalandadze and Rautian, 1983, 1984, 1993a). This was the greatest paleontologically documented global crisis in the assemblage of terrestrial (non-marine) tetrapods of the Early-Middle Jurassic time. It was not accompanied by marked crisis phenomena in other components of

land biota or, most of all, in flora, and the duration of its apogee exceeded noticably that of the biocenotic crisis in the mid-Cretaceous. Independently of us, M. Benton (1985, 1987, 1988) discovered the same crisis but, however, did not try to interpret it substantially. Data on this crisis allowed us to formulate the following:

(1) We put forth the concept of a considerable autonomy of the terrestrial tetrapod assemblages, which were not so much components of the concrete biocenosis but rather a community of harvest collectors, produced usually by several, sometimes by very many biocenoses. These considerations are consistent with the already-mentioned absence of the synchronous reaction of other components of the biota in the course of the Jurassic crisis and with the relatively weak reaction of vertebrates to the crisis in continental biocenoses of the mid-Cretaceous. Human beings, who historically came from the community of terrestrial tetrapods, demonstrate the same principal ecological strategy but in a monstrously hypertrophical manner: they are transformed into a kind of super-consumer of every resource, including unrenewable mineral resources of the Earth. The exact ecological strategy of the consumer, who is not very interested in the preservation of each separate producer that is, ultimately, the biocenosis, along with a rather weak dependence on the condition of each concrete biocenosis, has caused the confrontation of man with nature.

(2) We constructed a heuristic model of the conjugate evolution of the community and of its forming biota, with its taxonomical and ecological diversities. The model adds to the ideas of Zherikhin by the feed back mechanism, demonstrating the role of the phylogenesis processes in the formation, disruption during crisis, and reconstruction of the community structure, of its adaptive zones, and of ecological niches after the crisis.

The essential differences between these large ecological crises are evident. The first crisis embraces the biocenoses of the land as a whole, although not all of their components in equal degree. The second one concerns selectively all components of only a separate although large group of the organisms, which possess a considerable autonomy and specific function in the economy of the environment. The practically complete coincidence of the symptoms of these crises seems to be all the more significant. However, we must note, to avoid misunderstandings, that we consider only the qualitative coincidence of the symptoms. Some formal quantitative methods of analysis of the taxonomic and ecological diversity dynamics, which were applied to the fossil insect and tetrapod records, prove to be mutually inapplicable because of the phylogenetic, biocenotic, and taphonomic specifications of the above groups and the different degrees to which they are understood.

The interest in the study of the historical preconditions of the Jurassic crisis forces us, in particular, to analyze the previous smaller and essentially more transient ecological crisis in the terrestrial tetrapod assemblage, which took place at the very end of the Late Permian (Olson, 1989; Sennikov, 1991). The preliminary results of that work (Kalandadze and Rautian, 1992b, 1993c) testify that at least the larger part of the revealed symptoms are fulfilled in that case as well.

The first attempt at compiling the list of seven symptoms for the mid-Cretaceous crisis was caused by the necessity to compare them with those of the recently discovered Jurassic crisis. The qualitative coincidence proved to be perfect (Kalandadze and Rautian, 1983). For a more detailed analysis of the Jurassic crisis, the list of symptoms was doubled as a result of the works of both paleoentomologists and us. The coincidence was practically complete, as before; only the single symptom (1.5) dealing with the zoogeographical situation on the eve of the crisis is excepted (Kalandadze and Rautian, 1993a). The exception is conditioned by the absence of global zoogeographical reconstructions on insects for the Early Cretaceous. We made such reconstructions on terrestrial (non-marine and non-flying) tetrapods for the whole interval from the Carboniferrous to the Pleistocene (Kalandadze and Rautian, 1980, 1981, 1983, 1991, 1992a).

The interest that the enlarged list of the ecological crisis symptoms caused before its publication revealed a number of shortcomings in our list. The poor organization of the symptoms within the list produced a false impression of their independence; in actuality, they showed properties of an integrated syndrome (Fedonkin, 1991). The above-mentioned models, proposed by Zherikhin and us, were devoted to the demonstration of that circumstance as well. In the following list, we attempt to systematize more strictly and formulate more exactly the symptoms, though this cannot replace the arguments that are contained in the models.

In our previous versions of the list, we aspired to use when possible more empirical characteristics of the ecological crisis and to avoid those that were the results of reconstruction and could not be considered as direct evidence from the paleontological materials. It was apparent that the symptoms, empirical for paleontologists, are not applicable to recent ecological material because of the high specificity of the methods used in the study of the community evolution of the paleontological material. On the contrary, a matter that is the result of reconstruction for the paleontologist often can be the subject of direct observation for the neontologist.

This was the case when A.A. Vakhrushev (1988) tried to employ our models, which in fact are reconstructions of the processes known only by their traces in the paleontological record, to an analysis of the initial stages of development of communities of city birds. The city is known to be principally a new type of landscape, having no specific historically developed associations of organisms (Klausnitzer, 1990). Therefore, the first steps of the formation of such associations adequately model the initial stages of the recovery of the biocenosis structure after destruction in the course of an ecological crisis. In spite of the huge differences of the spatial, temporal, and taxonomic scales between the processes, reconstructed from the paleontological models and observed in the city's environments, Vakhrushev succeeded in confirm-

ing, with the recent material, a number of essential conclusions that follow from these models.

Taking into account the necessity of such "cross-traffic" in the ecological studies of the paleontological and neontological materials and trying to satisfy the demands of our colleague-neontologists, we included in the list the symptoms resulting from paleontological reconstruction, which can be the subject of direct observation or mediated research by the ecologist dealing with recent communities. The basis for these reconstructed symptoms is contained in cited publications devoted to the formulation of the models and their indirect control of the paleontological record. In this new form, the list of symptoms represents essentially the code of common characteristics (reconstructed and observed empirically from the paleontological record) revealed for the global crisis of the continental biocenoses in the mid-Cretaceous time and simultaneously for the largest paleontologically documented crisis of the terrestrial tetrapod assemblage in the Early-Middle Jurassic.

Thus, we submit for the reader's verdict a list of the symptoms of the ecological crisis, renewed strongly not only by form but by essence as well.

(1) The ecological crisis is preceded (the preparatory phase according to A.P. Rasnitsyn, 1988, 1989) by:

(1.1) An increase of the rate of taxa formation (cf. symptoms: 2.2.1, 2.2.2, 2.2.5, 3.2, and 4.2).

(1.2) An increase in the rate of extinction (first of all, of eurybiontic and less specialized cenophiles[1] at a rate surpassing that of taxa formation.

In consequence, an increase in the number of accumulated taxa is preserved (cf. synonyms: 2.1. 3.1, and 4.1).

(1.3) The appearance of interzonal lacunas[2] on the boundaries of the adaptive zones. A considerable portion of the lacunas either remain unclosed for a long time or are used by the predecessors of future active destroyers of the former community structure (cf. symptoms: 2.2.4 and 2.2.5).

(1.4) A decrease in the stability (an increase of the vulnerability) of formed communities to endogenic indignations and exogenic influences (cf. symptoms: 1.1 - 1.3, 1.6, 3.5, and 4.4).

(1.5) A relative continuum of the biota of all regions subject to the crisis. The historical-biogeographical "Pangea" precedes the global crisis.

(1.6) A large ecological crisis is preceded by a crisis of a smaller scale (cf. symptom: 4.4).

(2) The characteristics for the time environs of the ecological crisis are as follows (the preparatory, paradoxical, dramatic, and calming phases, according to Rasnitsyn, 1988, 1989):

(2.1) The extinction of a large number of taxa formerly widespread, including those of higher ranks (cf. symptoms: 1.2, 3.1, and 4.1).

(2.2) The appearance:

(2.2.1) of a large number of taxa, including those of higher ranks (cf. symptoms: 1.1., 3.3, and 4.2);

(2.2.2) of a large number of short-ranged taxa (reported in the paleontological record), including those of the comparatively higher ranks, (mainly, of a family level during a large crisis (cf. symptoms: 1.1, 3.2, and 4.2);

(2.2.3) of taxa reported regularly in the paleontological record only in the time environs of the crisis (cf. symptoms: 3.4 - 3.8);

(2.2.4) of large ecological innovations that had essential consequences in the further history of the biosphere, in the case of the large crisis (cf. symptoms: 1.3 and 2.2.5);

(2.2.5) of the majority of the future ecological dominants either before or after the crisis (cf. symptoms: 1.1., 3.2, and 4.2).

(2.3) An increase in a share of taxa reaching the present and a decrease in their taxonomic rank (cf. symptoms: 2.4 and 2.6.).

---

[1] The terms *cenophiles* and *cenophobes* were introduced by S.M. Razumovskii (1981) to designate plant species, respectively, included in the succession system and not included in it. The property of being a cenophile or cenophobe refers not to the species on the whole, but to the living form, in this case, to the role of the cenopopulation of the species in the phytocenosis of the present botanic-geographical area. The species can be a cenophile in one botanic-geographical area and a cenophobe in a neighbouring area, and vice versa. We use these terms in a wider sense (Kalandadze and Rautian, 1993a), keeping the spirit of the first definition but not its letter.

Cenophiles are the living forms of the organisms, specialized during the preceding coevolution to a life in the conditions of quite definite biotic and abiotic settings (environment). They constitute the community of organisms formed during the preceding phylogenesis. The structure of the adaptive zones and ecological niches of the community is stable, reproduced by self-assembly from taxa of the characteristic biota (the flora and fauna) in the historically typical conditions (Shmal'gauzen, 1968) of the environment, called an ecotope (Rautian, 1993). The cenophiles are more competitive, but only in conditions historically typical of their community. The motto of the adaptive strategy of the cenophiles is, "our power is in the coordination of our actions."

The cenophobes are the living forms of organisms surviving successfully in various (poorly predicted) conditions of rather unstable (uncertain) abiotic and biotic environments. In contrast to complex communities, they form groups of organisms, indefinite both in composition of the biota and in structure of the adaptive zones and ecological niches. The groups are characteristic of environments disturbed or newly arisen as the results of geological processes and have not been captured or are unfit for the life of the formed community. The wide spectrum of the different habitations but low level of specialization and competitive ability in a particular biotope, which they can occupy only in the absence of competitive pressure from the specialized cenophiles, is characteristic of cenophobes. The motto of the adaptive strategy of the cenophobe is "every life form for itself."

[2] Interzonal ecological lacunas are the boundary regions of the adaptive zones, extremely poorly defend their highly specialized stenobiotic owners and, are therefore, accessible to the less specialized forms from ecotones because of their euvrybiontity, but inaccessible to specialized stenobiotic cenophiles. Interzonal lacunas arise as a result of a mutually stipulated increase in the stenobiontity and competitive ability of the owners of the adaptive zones in the process of their phylogenetic specialization and of the competitive ouster of less specialized and, therefore, less competitive euryobiontic cenophiles (Kalandadze and Rautian, 1984, 1993a).

(2.4) A vicarious replacement of a number of ancient taxa of high rank by phylogenetically successive taxa of the same rank (cf. symptom: 2.6).

(2.5) An increase in the share of the phylogenetic relicts leading to the obsolescence of some the biota, which is particularly characteristic for the climax of the crisis (cf. symptoms: 3.4 - 3.8).

(2.6) A change in the ecological dominants, which is expressed in the transformation of a number of taxa from the category of the rare and the rarest to the category of those regularly reported in the paleontological record and vice versa (cf. symptom: 3.5).

(2.7) A sharp change in the taxonomic composition of the biota (moreover, even sharper for a large crisis) and in the composition of the living forms of the dominant types of communities during the relatively short interval of the geological time (cf. symptoms: 1.1, 1.2, 2.1 - 2.6, 3.2, 3.3, 4.1, and 4.2). This symptom is an exceptional expression of the principle of threshold reaction of W.R. Ashby (1959, 1962) and testifies indirectly to the stability of the communities of organisms in the geologically long intercrisis epochs.

(3) The characteristics for the climax of the ecological crisis are as follows (the paradoxical phase according to Rasnitsyn, 1988, 1989):

(3.1) Some decrease in the rate of extinction due to symptom 3.4 (cf. symptoms: 1.2 and 4.1).

(3.2) A sharp decrease in the rate of taxa formation, surpassing the decrease in the rate of extinction and leading to a reduction in the number of accumulated taxa (not only species and genera, but also families in a large crisis; cf. symptoms: 1.1, 2.2.5, and 4.2).

(3.3) A sharp decrease in biota diversity, which is connected not so much with an increase in the rate of extinction of the taxons as with a decrease in the rate of their appearance (cf. symptom: 3.2).

(3.4) A decrease in the intensity of the factors in the struggle for existence, depending on the population density (cf. symptoms: 2.2.3, 2.5, and 3.1).

(3.5) A destruction of the former structure of the communities: the succession system (if it is present in a given type of community) and the structure of the adaptive zones and ecological niches (cf. symptoms: 1.4 and 4.4). Thus, the cenotic limitations of the phylogenesis[3] are removed in proportion to the degree of the destruction of the community structure.

(3.6) A loss of the conformity of the phylogenetic and ecological specialization of a number of taxa due to symptom 3.5 (a great many of taxa in the course of a large crisis).

(3.7) A decrease in the ecological valence and an increase in the probability of extinction of the highly specialized cenophiles due to symptoms 3.5 and 3.6 (especially in the next stage of phylogenesis because of symptom 4.3).

(3.8) An increase in the ecological valence and a decrease in the probability of the less specialized and eurybiontic forms of ecotones, first of all, cenophobes, due to symptoms 3.5 - 3.7 (especially in the next stage of the phylogenesis because of symptom 4.3).

(3.9) A falling out of a number of taxa, remaining without any significant changes during the crisis, from the geological record due to symptoms 3.5 - 3.7.

(3.10) An active approach of ecotones to the preserved areas of the formed communities due to symptoms 3.5 - 3.8.

(3.11) A variegated mosaic of the areas, which preserved, to some degree, the former biota and the community organization, and of the spacious ecotones, which have an indefinite biota composition. The biota includes the ancestors of the future ecological dominants of the postcrisis communities (cf. symptoms: 3.5 and 3.10).

(3.12) A wide geographical representation of the localities, which is accompanied by a low diversity of their biotas and weak biogeographical connections between the taxa because of the rarity of their repeated finds in various sites (cf. symptoms: 3.3 and 3.11).

(4) The ecological crisis is completed by (the dramatic and calming phases, according to Rasnitsyn, 1988, 1989):

(4.1) An increase in the rate of extinction due to symptom 4.3.

(4.2) A sharp decrease in the rate of formation of taxa, which outstrips that of extinction. In consequence, an increase in the accumulation of the number of taxa is restored (cf. symptoms: 1.1 and 3.2).

(4.3) An increase in the intensity of the factors in the struggle for existence, which are dependent on the population density (cf. symptom: 3.4).

(4.4) The appearance of a new biota (a new type community), which, if it was preceded by a large crisis, would be short-lived and would be affected by a new crisis but of smaller scale shortly (in the geological sense) after its appearance (cf. symptom: 1.6).

[3] The cenotic limitations of the phylogenesis are the limitations of the phylogenesis of taxa, connected with the presence of: (1) a definite ecological niche or adaptive zone, which appeared during the preceding phylogenesis and (2) a community with the definite structure of a succession system, adaptive zones, and ecological niches, which appeared during the preceding phylogenesis in its biotic surrounding (environment). The destruction of the community structure during the ecological crisis, which affects the inner structure of the adaptive zones and ecological niches of taxa that make up the community, removes at least a part of the cenotic restriction of the phylogenesis of the last ones. V.A. Krasilov (1969) called the evolution (phylogenesis) occurring under the hard cenotic restriction of the formed community (Vakhrushev, 1988) a coherent evolution. He named the evolution occurring without such a control, incoherent evolution. (Rodendorf and Zherikhin, 1974; Zherikhin, 1978 - 1987; Zerikhin and Rasnitsyn, 1980; Rasnitsyn, 1988 - 1990).

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Geochemistry and Age of Aluminiferous Gneisses of the Archean Kola Group of the Baltic Shield

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Abstract – The results on geochemistry and Rb-Sr isotope dating of the aluminiferous gneisses of the Central Kola granulite-gneiss region are given. The age of rocks is estimated to be 2880 ± 50 Ma. The low value of the initial isotopic ratio $(^{87}Sr/^{86}Sr)_0 = 0.7005 \pm 0.004$ permits the assumption that the original sedimentary rocks were formed from the material of the primary crust (the product of the mantle magmatism) during an extremely short period of time. The chemical composition of the rocks and the data on the oxygen isotope composition support this assumption.

One of the most urgent problems of Precambrian geology is to define the conditions of the formation and evolution of the granulite-gneiss regions. It is obvious that this problem cannot be solved without detailed isotopic and geochemical studies. The necessary data is least available for highly metamorphosed sedimentary rocks. However, their study is especially important, as the data on the sedimentary formations can be used to understand the nature of the Archean upper crust (Taylor *et al.*, 1988).

This work presents some new data on the geochemistry and Rb-Sr isotope data of the aluminiferous gneiss of the Kola group – one of the most important of the Archean subdivisions stratigraphy of the northeastern part of the Baltic shield. It composes the Central-Kola granulite-gneiss region, represented by para- and orthorocks metamorphosed in granulite and amphibolite facies. We used this data to determine not only the age of the gneisses, but also the sources of the material and the conditions under which these metasediments were formed.

The Central-Kola region is situated in the axial part of the Kola Peninsula (Fig. 1), stretching in a northwestern direction more than on 250 km with average width for about 60 km. In the northeast and southwest, it borders the Archean greenstone belts, the Kolmozer–Voron'e and Olenegorsk–Tal'e, respectively (Avakyan *et al.*, 1984; Avakyan, 1992; Dobrzhinetskaya, 1989). The northwestern part of the region is composed mainly of pararocks: garnet–biotite, sillimanite–cordierite–biotite–garnet and other gneisses, strongly subordinated ferruginous quartzites, and highly metamorphosed calc-siliceous rocks. In the central part of the peninsula, these pararocks are closely associated with orthorocks, represented by enderbites, basic crystalline schists, and metapyroxenites in the granulite zone, and by biotite–amphibole plagiogneisses, amphibolites, and hornblendites in the zone of the amphibolite facies of metamorphism. Here they occur as a set of alternating tectonic sheets, dipping in the direction of the adjacent greenstone belts (Avakyan *et al.*, 1984; Avakyan, 1988, 1992; Dobrzhinetskaya, 1989). The decrease of metamorphic grade from the granulite to the amphibolite facies is reported as occurring in the same direction (Avakyan, 1992).

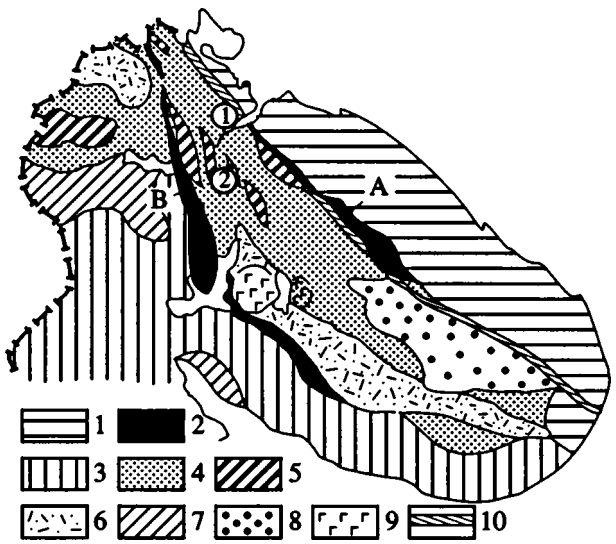

Fig. 1. *The scheme of distribution of the Early Precambrian complexes in the Kola Peninsula.*
1 - 5 – the Archean rocks: 1 – the Murmansk granite–gneiss complex, 2 – supra–crustal complexes of the Kolmozero–Voron'e (A) and Olenegorsk–Tal'e (B) greenstone belts, 3 – the Belomorsk complex, 4 – the complex of para-, and 5 – orthorocks of the Central-Kola granite–gneiss region; 6 - 8 – the Early Proterozoic rocks: 6 – supra–crustal complexes of the Pechenga and Imandra–Varzuga greenstone belts, 7 – the Lapland–Kolva granulite complex, 8 – the Keivozero complex; 9 – the Paleozoic complex of the nepheline syenites; 10 – the zone of the Murmansk strike-sleep fault. Figures in circles show the sampling locations: 1 – the area of the Tulp'yavr Lake; 2 – the Murdozero area.

The relationships of the Central-Kola granulite–gneiss area and the continuous greenstone belts are not clear, but the boundaries between them are gradual. The calc-alkaline orthorocks of granulite and amphibolite facies are replaced by the poorly metamorphosed metavolcanites of tholeiitic and comatiitic composition, whereas the chemical composition of the pararocks changes only slightly.

Para- and orthorocks were repeatedly subjected to joint deformations. At present, they are characterized by a single style of tectonic structure. The deformations took place in the background of regional metamorphism, being accompanied by the migmatization of the sodium specialization in the orthorocks and of the potassium specialization in the pararocks (Avakyan, 1992).

The age of metamorphism was repeatedly determined using U-Pb methods on zircons from orthorocks: 2700 ± 50 Ma (Tugarinov and Bibikova, 1980), 2830 ± 15 Ma (Pushkarev *et al.*, 1979), and 2770 ± 20 Ma (Gracheva *et al.*, 1985). The latter work also gives the minimum age of "magmatogenic" zircons from the basic granulites as 2850 ± 30 Ma. The age of the aluminiferous gneiss (2660 ± 40 Ma) was determined using the bulk-rock Rb-Sr method (Gorokhov *et al.*, 1976). The new data following below on the strontium and oxygen isotopes and trace elements elucidate, to some extent, the time and the conditions under which the aluminiferous gneisses of the Kola group were formed.

The samples were collected in two areas, spaced apart by almost 70 km (Fig. 1). The rubidium–strontium system was studied in 11 samples. Six of them (nos. 1 - 6 in Tables 1, 2, and 3 and Fig. 3) were collected in the northwestern part of the Central-Kola region in the area of Tulp'yavr Lake, and the remaining five samples (nos. 7 - 11) are from the vicinity of Murdozera, situated in the central part of the region.

The aluminiferous gneisses are represented by fine- to medium-grained garnet-biotite (nos. 4, 5, 9, and 10) and coarse-grained sillimanite–cordierite–garnet (no. 7) varieties. Quantitative (Table 1) and chemical compositions of minerals vary over wide limits. The (Mg/(Mg + Fe)) index of garnet, biotite, and cordierite from the gneisses of the Tulp'yavr Lake area (0.21 - 0.32; 0.58 - 0.65; 0.75 - 0.76, respectively) is much lower than in the similar minerals of the Murdozera area (0.39 - 0.48; 0.73 - 0.83; 0.84 - 0.91). The calculations made using mineral geothermometers (Fonarev *et al.*, 1989a, 1989b) make it possible to explain this discrepancy by a lower grade the rocks of metamorphism of the northwestern part of the granulite–gneiss area: $T = 580 \pm 30$°C, $P = 4 \pm 0.5$ kbar – for the rocks from the Tulp'yavr vicinity; $T = 680 \pm 20$°C, $P = 6 \pm 1$ kbar for the gneisses of the Murdozera area.

Apart from the aluminiferous gneiss, we analyzed the following rocks (Tables 1, 2, and 3; Figs. 2 and 3): synmetamorphic garnet–bearing granite, composing leucosome in the migmatized gneisses; bronzite–bytownite rock (metamorphosed calc-siliceous rock) forming, along with ferrugineous quartzites, rare thin interlayers in the aluminiferous gneisses; and biotite plagiogneiss, distributed only in the zones of the amphibolite facies metamorphism.

The chemical composition of the aluminiferous gneisses is monotypic in both of the studied areas (Table 2). Compared to the average Archean argillaceous schists (Taylor and McLannan, 1988), the studied gneisses have higher contents of rare earth elements, U, Th, Hf, and Zr (Fig. 2a). The REE distribution patterns are strongly fractionated (La/Yb)N = 6.3 - 27.6, having negative europium anomalies, which are not typical for the Archean sedimentary rocks. Moreover, they are characterized by a low K/Rb ratio, unusual for granulites.

As distinct from the aluminiferous gneisses, the garnet-bearing granites (Fig. 2b) have a positive europium anomaly, are more strongly depleted in heavy rare earth elements, and have lower values of Zr, Hf, Sc, and Co (Table 2). The biotite plagiogneiss and

Table 1. Quantitative mineral rocks composition

Numbers in succession	Sample number	Composition, volume %
1	TD4	P1(43)–Q(12)–Bi(15)–Ga(10)–Ksp(8)–Crd(7)–Sil(5)–Op(<1)
2	TD5/1	P1(40)–Bi(23)–Ga(22)–Sil(7)–Q(5)–Ksp(3)–Op(<1)
3	TD5/2	P1(38)–Ga(22)–Bi(14)–Sil(8)–Crd(8)–Ksp(5)–Q(5)–Opx(<1)
4	TD5/3	P1(53)–Q(26)–Bi(13)–Ga(7)–Sil(1)–Op(<1)
5	TD5/4	P1(49)–Q(31)–Bi(11)–Ga(8)–Sil(1)–Op(<1)
6	TD8	P1(54)–Q(32)–Bi(14)–Op(<1)
7	217/1	P1(30)–Ga(22)–Bi(18)–Q(10)–Crd(8)–Sil(5)–Ksp(7)–Spl(<1)
8	217/2	P1(49)–Opx(44)–Cpx(5)–Q(2)–Op(<1)
9	460/1	P1(58)–Q(23)–Bi(12)–Ga(7)
10	474/2	P1(40)–Ga(19)–Bi(16)–Q(15)–Ksp(9)–Crd(1)–Op(<1)
11	474/3	P1(52)–Q(33)–Ksp(6)–Ga(6)–Bi(3)

Note: Q – quartz; Bi – biotite; Ga – garnet; Pl – plagioclase; Ksp – potassium feldspar; Sil – sillimanite; Crd – cordierite; Spl – spinel; Opx – orhtopyroxene; Cpx – clinopyroxene; Op – opaque minerals.

Table 2. The chemical composition of the aluminiferous gneisses (1 - 5, 7, 9, 10), biotite plagiogneiss (6), bronzite–bytownite rocks (8), and garnet plagiogranite (11)

Components	1 TD4	2 TD5/1	3 TD5/2	4 TD5/3	5 TD5/4	6 TD8	7 217/1	8 217/2	9 460/1	10 474/2	11 474/3
SiO_2(%)	62.06	52.04	56.00	69.06	70.24	66.37	62.55	49.75	66.35	61.89	71.25
TiO_2	0.89	1.12	1.03	0.80	0.69	0.96	0.70	0.60	0.48	0.72	0.30
Al_2O_3	18.18	24.50	21.68	14.21	14.12	15.03	17.49	11.35	16.07	16.85	15.38
FeO*	7.85	10.13	8.70	4.96	4.87	5.86	6.57	13.80	5.41	7.72	2.12
MnO	0.05	0.09	0.07	0.07	0.05	0.08	0.04	0.05	0.07	0.04	0.02
MgO	4.00	4.53	3.69	1.92	2.49	1.14	3.75	13.31	2.82	3.92	1.06
CaO	1.15	1.35	1.61	3.01	1.52	3.99	2.05	10.88	4.16	1.78	2.51
Na_2O	2.12	1.77	2.22	3.12	3.04	4.78	2.80	0.49	3.12	2.92	4.80
K_2O	2.39	2.55	2.50	1.93	1.51	1.00	2.24	0.37	1.30	2.60	1.33
P_2O_5	0.03	0.10	0.13	0.07	0.01	0.20	0.01	0.01	0.18	0.01	0.01
Loss on ignition (l. o. i.)	0.38	0.31	0.40	0.31	0.10	0.52	0.19	not found	0.24	0.21	not found
Total	99.10	98.49	98.03	99.46	98.64	99.93	98.39	100.61	100.20	98.66	98.78
La(g/t)	34	30	60	42		23	48	3.7	45		36
Ce	60	60	100	87		43	100	6.6	88		71
Sm	5.4	5.9	9	6.2		7.0	7.5	1.7	7.2		4.0
Eu	0.96	0.93	1.1	1.2		1.0	1.1	0.48	1.2		1.7
Tb	0.69	0.91	1.00	0.87		1.1	0.88	0.36	0.59		0.56
Yb	2.5	3.2	2.0	2.1		3.7	2.0	1.4	1.1		0.85
Lu	0.45	0.47	0.33	0.29		0.64	0.27	0.19	0.20		0.11
Rb	105	116	105	56	52	15	103	12	76	102	43
Sr	187	237	222	197	206	109	298	116	643	226	366
Ba	700	660	680	460		240	480	42	630		290
Hf	5.8	5.0	4.7	8.9		5.9	4.0	1.4	4.0		<2
Zr	160	150	180	200		15	103	12	130		33
Ta	0.67	0.10	1.00	0.50		0.50	0.42	0.20	0.5		<0.5
Nb	9.3	9.3	7.8	6.9		8.7	8.9	1.4	6.5		2.4
U			2.4	2.3		1.0			3.2		1.2
Th	16	11	10	9.1		2.9	34	2	8.8		3.6
Y	23	23	20	15		30	19	14	10		5.3
Sc	26	40	37	18		13	21	51	11		7.1
Co	20	16	45	30		9.8	16	59	12		11
Cr	240	290	270	500		150	150	1100	320		150
K/Rb	189	183	198	286	241	553	181	256	142	212	257
Rb/Sr	0.56	0.49	0.47	0.28	0.25	0.14	0.35	0.10	0.12	0.45	0.12
La/Th	2.1	2.7	6.0	4.6		7.93	1.4	1.85	5.1		10
La/Sc	1.3	0.8	1.6	2.3		1.77	2.3	0.07	4.1		5.1
$(La/Yb)_N$	9.18	6.33	20.26	13.50		4.20	16.20	1.78	27.6		28.6

Note: FeO – all iron is given as FeO. In the numerator – the ordinal number, in the denominator – the sample number. 1 - 6 – Gneisses of the amphibolite facies from the central part of the area (the Murdozera area). Major oxides in %; trace in ppm.

bronzite-bytownite rock are sharply distinguished from the above rocks by their chemical composition (Table 2, Fig. 2b).

The study of the orthorocks related to the complex of the aluminiferous gneisses and other metasedimentary rocks showed them to be of the highly metamorphosed volcano–plutonic association of the contrast gabbro–tonalite composition (Avakyan, 1988, 1992). All the orthorocks are referred to the calc-alkaline series; they are enriched in light rare earth elements,

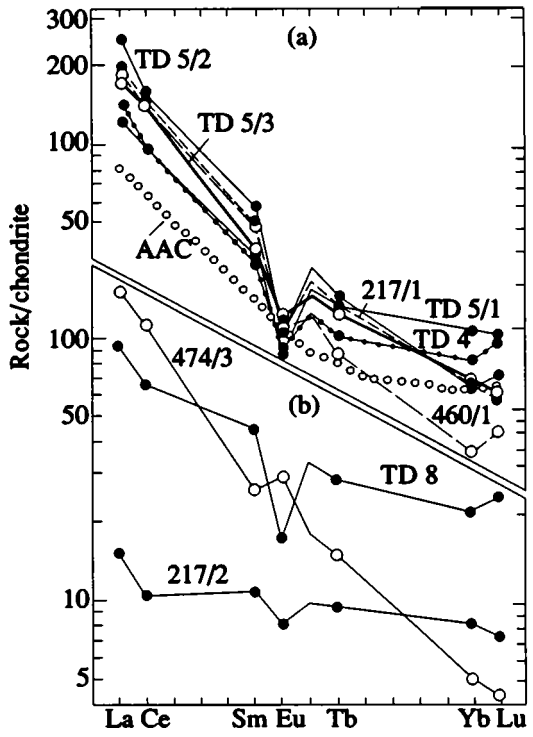

Fig. 2. *The REE distribution in the aluminiferous gneisses (a) and associated rocks (b): garnet-bearing granite – 474/3, biotite plagiogneiss – TD-8, bronzite-bytownite rock – 217/2.* AAC – the average Archean claystones (Taylor *et al.*, 1988). Normalized according to (Evensen *et al.*, 1978).

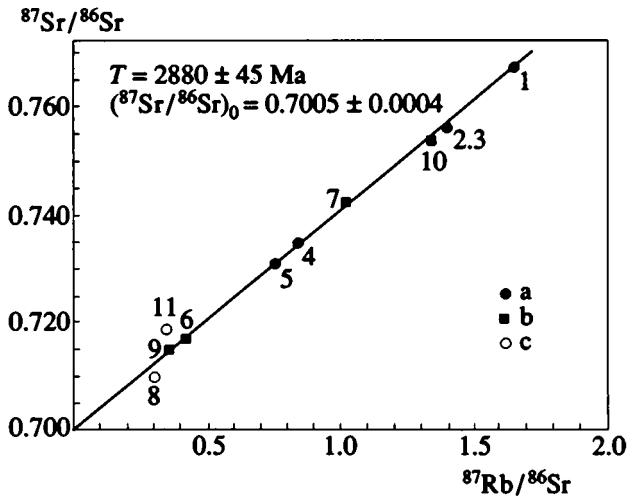

Fig. 3. *The bulk-rock Rb-Sr isochrone for the aluminiferous gneisses of the Kola group.*
a – gneiss from the Tulp'yavr Lake area; b – gneisses from the Murdozera area; c – points, not plotting on the isochrone.

having a small negative europium anomaly. Judging by the contents of microelements, the protolith of the aluminiferous gneisses could have been formed as a result of the erosion of this bimodal complex (Avakyan, 1992). In particular, the negative europium anomalies in the aluminiferous gneisses of the Kola group could be inherited from the initial igneous rocks. The sedimentary rocks seem to be formed simultaneously with the volcano–plutonic complex, as its terrigenous facies. Other possible source material in the region is unknown.

The isotope measurements were made using a MAT 260 mass-spectrometer in the Isotope Geochemistry and Geochronology Laboratory, Geological Institute, Russian Academy of Sciences. The main features of the used experimental techniques are described in *Geokhimiya...* (1993). The $^{87}Sr/^{86}Sr$ ratio and Sr and Rb concentrations were determined by the double isotope dilution method using a mixed ^{84}Sr–^{87}Rb spike. The Rb and Sr separation was made from the aliquots of samples dissolved in about 200 mg of acid by the ion-exchange chromatography. The error of $^{87}Rb/^{86}Sr$ ratio determination is about 1.5%; the accuracy of the $^{87}Sr/^{86}Sr$ isotope ratio measurement is not less than ±0.0001. The ratios obtained are normalized to $^{88}Sr/^{86}Sr = 8.37521$.

The results of the measurements are given in Table 3 and in Fig. 3. The graph shows that nine points plot well along a straight line constructed using the χ^2 method (Sokolov and Buyakaite, 1986). Evidence of the consistency of the linear dependence model based on the χ^2 method is the relationship between the normalized sum of the squared deviations ($S = 9.84$) and the permissible limit values for a given set of the data points ($\chi^2 = 11.07$). The isochrone model is regarded to be consistent with $S_{min} < \chi^2$. Additional evidence supporting the age interpretation of the straight line is the lack of correlation in $^{87}Sr/^{86}Sr$–I/Sr coordinates (Faure, 1989).

Thus, giving the line an age interpretation, we estimate an age of 2880 ± 50 Ma and an initial ratio of $(^{87}Sr/^{86}Sr)_0 = 0.7005 + 0.0004$. The two points, corresponding to the synmetamorphic garnet-bearing granite and bronzite-bytownite rock, deviated from the straight line in different directions (Fig. 3). Presumably, this occurred due to the younger granite age and different initial ratio of $(^{87}Sr/^{86}Sr)_0$ in the metamorphosed calc-siliceous rock.

It should be particularly emphasized that if all the points forming the isochrone are divided into two groups corresponding to the granulite and amphibolite zones of metamorphism, two straight lines will be obtained, having practically identical characteristics, respectively: $T = 2900 \pm 80$ Ma, $I_0 = 0.7004 \pm 0.0006$, and $T = 2870 \pm 50$ Ma, $I_0 = 0.7005 \pm 0.0005$. This fact along with the geological evidence prove the consistency of the joint age interpretation of the rocks from the two areas, different in metamorphic grade and spaced apart by 50 km, of the Central-Kola granulite-gneiss region.

The bulk-rock isochrone, established for metasediments, is known to show the time of the isotopic homogenization, which, in its turn, can comply with the age of the source rocks or with the age of diagenesis or metamorphism of the sedimentary rocks (Faure, 1989).

Table 3. Rubidium, strontium, oxygen, and their isotopes in the pararocks of the granulite-gneiss in the Central-Kola region

Numbers in succession	$^{87}Sr/^{86}Sr$	$^{87}Rb/^{86}Sr$	Rb, g/t	Sr, g/t	$\delta^{18}O$, ‰
Tulp'yavr Lake area					
1	0.76885(875)	1.6288	104.8	187.3	7.7
2	0.75680	1.3812	113.4	238.7	–
3	0.75679	1.3822	105.4	221.8	–
4	0.73563	0.8226	55.75	196.6	9.0
5	0.73187	0.7369	52.43	206.3	–
6	0.71691	0.4011	15.15	109.4	–
Murdozera area					
7	0.743188	1.0062	103.4	298.3	9.4
8	0.70981	0.2976	11.92	115.9	8.9
9	0.71483	0.3442	76.4	642.9	9.3
10	0.75475	1.3084	101.6	225.7	–
11	0.71881	0.3352	43.2	366.1	–

Note: $\delta^{18}O$ – according to B.G. Pokrovski (Geologal Institute), Russian Acad. of Sci.).

Hence, the interpretation of such isochrones requires additional data.

The dating obtained is one of the oldest for the region in question. It is much older than the age of "metamorphogenic" zircons and coincides within analytical error with the age of "magmatogenic" zircons from the orthorocks of the same complex (Gracheva *et al.*, 1985). We can assume, therefore, that during the regional metamorphism of the granulite and amphibolite facies, which occurred 2.7 Ga ago, the Rb-Sr rock system, as a whole, remained closed, in spite of the isotopic homogenization in the minerals and complete recrystallization of the initial argillaceous sediments. The age determination of the metamorphism, using Rb-Sr mineral isochrone, could make things more clear, but this task is beyond the scope of this study. Thus, the age of 2880 ± 50 Ma most probably corresponds to post-sedimentation diagenetic process and initial thermal metamorphism and recrystallization rather than to regional metamorphism and the age of the source rocks (this is possible only under the presence of detrite minerals). The initial isotope homogenization of sedimentary rocks is usually related to these very processes (Faure, 1989).

The low initial $^{87}Sr/^{86}Sr$ ratio in the aluminiferous gneisses is noteworthy. It is of interest that on the strontium evolution diagram ($^{87}Sr/^{86}Sr$-time), this initial ratio with $T = 2900$ Ma is near the evolutionary line of the depleted mantle material. The published data available (Faure, 1989) shows that $^{87}Sr/^{86}Sr$ ratios in the Archean carbonate rocks (in the surface waters as well) were similar to those in the mantle. This can be explained by the fact that the rocks exposed on the surface were young, having a low initial Rb-Sr ratio. In other words, the sedimentary rocks were formed from the material of the primary crust (the product of the mantle magmatism) during an extremely short time interval. A plausible material might be the protolith of the Kola group orthorocks. Thus, the data on strontium isotopic composition in the aluminiferous gneisses refutes the possibility that an older sialic crust existed in this region.

The oxygen isotope composition (Table 3) supports this assumption. The low values of $\delta^{18}O = 7.7 - 9.4$‰, established in the aluminiferous gneisses and metamorphosed calc-siliceous rock, are typical for the immature sediments. These values are not much higher than those in the orthorocks of this region (Bibikova, 1989).

Thus, the similarity between the age of the aluminiferous gneiss, established using the bulk-rock Rb-Sr method, and the age of the magmatic zircons from the basic schists dated by the U-Pb method (Gracheva, 1985), correspond with the earlier published geological and geochemical data (Avakyan, 1992), indicating that the protolith of the aluminiferous gneisses might have been formed because of the erosion of the bimodal gabbro–tonalite volcanic association, represented at present by the complex of orthorocks.

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The Age of the Jotnian Magmatism of the North Ladoga Region

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Abstract – New age data obtained by the Rb-Sr isochrone method for the intermediate basic rocks of the Hopunvaara intrusion (1330 ± 50 Ma) are of great stratigraphic importance, as they specify the age of the Jotnian rocks in the North Ladoga region. They also indicate that the above magmatic formations belong to the first impulse of the Jotnian magmatism, synchronous with the processes of the sedimentagenesis in the Jotnian graben–synclines of the Baltic shield. In petrochemistry and isotope-geochemistry, the Jotnian magmatic rocks of the North Ladoga region are similar to the typical intraplate continental basalts.

The Jotnian magmatic rocks occur in a limited amount in the area of the Baltic shield, primarily in its southern part, forming a wide belt of minor intrusions, dikes, sills, and volcanic rocks of basic composition, stretching along the boundary of the East European platform. The magmatic activity of that time commonly took place within the epicratonic superimposed basins of the graben–syncline type, composed of rudaceous, poorly sorted, red terrigeneous rocks. In Finland, it is the Stakunta basin, in Sweden, the Jotnian complex of the Dala structure, and in Karelia, the Pasha graben, situated in the Ladoga Lake region. These Jotnian graben–synclines are spatially associated with earlier intrusions of the anorthosite–rapakivi granitic formation of the Gothian tectono-magmatic cycle and with the volcano-plutonic structures of the Transscandinavian granite–porphyry belt.

The geochronological data for the western part of the Baltic shield (Welin, 1975; Patchett, 1978; Lundqvist, 1979; Simonen, 1980) testifies to the two impulses of the Jotnian magmatism (1350 - 1370 Ma and 1212 - 1275 Ma) and to the age of the Jotnian sedimentary rocks (Rb-Sr and K-Ar methods) of about 1300 - 1400 Ma according to Simonen (1980). Dikes of the Tuna-dolerites of the Southern Dalarna areas (Sweden) were intruded in the course of the first impulse. According to P.J. Patchett (1978), their Rb-Sr age (by the bulk-rock isochrone) is 1371 ± 50 Ma. Acid dikes (Gustaf porphyries) of the same age are also associated with this impulse. The initial $^{87}Sr/^{86}Sr$ ratio for these magmatic rocks is 0.703 ± 0.002.

A similar K-Ar age (~1350 Ma) is reported for the main Salmi volcanites of the Pasha graben in the North Ladoga region (Khazov, 1973). But this age cannot be reliable, as it was published without presenting the original analytical data and the materials used for the isotopic studies.

The second impulse of magmatism is responsible for the intrusion of basic dikes and sills, which are rather widespread in the area of Central Sweden and Southwestern Finland, unlike the locally occurring dikes of the first magmatic impulse. In Sweden, they consist of olivine dolerites of Asby and Sarna type, which are frequently associated with granophyres of reomorphic origin and hybrid rocks of monzonite composition. According to P.J. Patchett (1978), the Rb-Sr age of these rocks (by the bulk-rock and mineral isochrones for 13 areas) averages about 1220 Ma, with variations from 1156 ± 15 to 1247 ± 18 Ma. The initial $^{87}Sr/^{86}Sr$ ratio in the least contaminated dolerites is 0.7032. A nearly identical age of 1215 Ma was obtained using the K-Ar method (the bulk-rock and mineral isochrone) for the dolerite dikes of the Vasternorrland area (Cleasson, 1987) and the rhythmically-layered sill of the Ulvo dolerites in the Southern Norrland area (Welin, 1975). Similar ages (1250 - 1270 Ma, Rb-Sr method and U-Pb dating on zircons) for the diabase of the Satakunta basin in Finland were published by Q. Simonen (1980), but without the original analytical data.

In the North Ladoga region, the Jotnian magmatic rocks, referred to the trachybasalt formation (Geologiya..., 1987), comprise the volcanic complex of the olivine-basalt lava sheets of the Salmi formation, the dike basaltoid complex, the Valaam layered sill, composed of rocks variable in composition from sub-alkaline gabbro to quartz-monzonites, granodiorites and aplitic granites, and the small Hopunvaara subvolcanic intrusion. The geochronological studies of the Jotnian magmatic rocks of the North Ladoga region were conducted only for basalts of the Salmi Formation using the K-Ar method. In the work of A.I. Kairyak and R.A. Khazov (1967), essentially different datings, obtained in the different laboratories, are given: 1100 - 1300 Ma (Institute

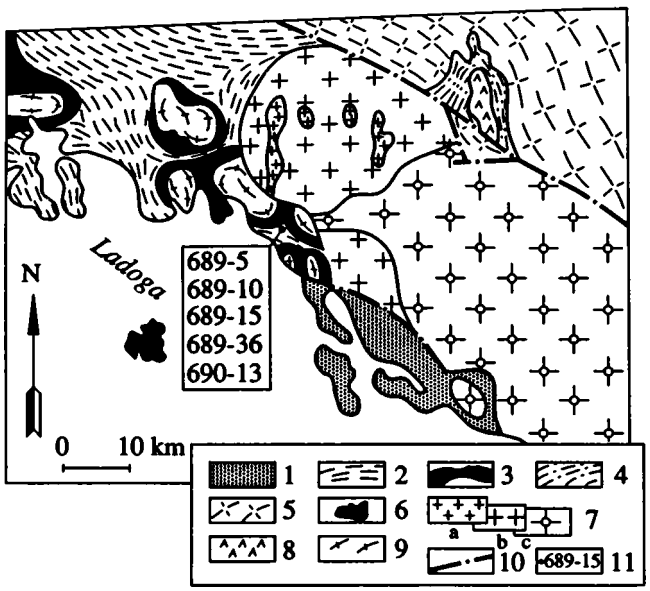

Fig. 1. *The scheme of geological structure of the northeastern part of the Ladoga region.*

1 – the Jotnian volcanologenic-sedimentary complex (the Salmi Formation); 2 - 4 – Early Proterozoic karelid formations: 2 – quartz–biotite, highly aluminous and other schists (the Ladoga Group), 3 – amphibole schists, amphibolites and quartzites with marble and scarn horizons (the Pitkaranta Formation), 4 – carbonate–terrigeneous–volcanogenic complex (the Tulomozero Formation); 5 – supracrustal and granitoid formations of the Karelian granite–greenstone region (AR_2); 6 – Jotnian intrusions of the intermediate-basic composition; 7 – the Salmi massif of the rapakivi granites (PR_2): a – fine-grained biotite granites; b – medium-grained biotite granites; c – coarse-grained biotite–amphibole granites; 8 – gabbro–diabases (PR_1); 9 – granite–gneiss domes (AR_2–PR_1); 10 – faults; 11 – locations of geochronological sampling.

of Geochemistry and Analytical Chemistry) and 1500 Ma (The Laboratory of Precambrian Geology, Russian Acad. of Sci.). In Khazov's more recent monograph, an age of 1350 Ma is given. At present, all of these data can be regarded only as conditional.

The objective of this work was to date the Jotnian magmatic rocks of the North Ladoga region using the Rb-Sr isochrone method. Geologically, the volcanites of the Salmi formation appear to be the most suitable for this purpose, being clearly of the same age as the terrigeneous rocks of the formation in question. The geological position of the Salmi Formation is quite clear: its nonmetamorphosed and unfolded rocks lie over the weathering crust after the rapakivi granite of the Salmi massif. The granite age of the Salmi massif was determined as 1550 ± 30 Ma by Schergina *et al.* (1982) using a combination of methods (K-Ar, Pb-Pb dating on zircons, Rb-Sr isochrone method). Later, it was estimated as 1543 ± 8 Ma using the U-Pb isochrone method on zircons (Neymark *et al.*, 1991). The lithologo-stratigraphic investigations carried out by Kairyak and Khazov (1967) proved the validity of their identification with typical Jotnian rocks of Sweden and Finland. These basalts, however, are unsuitable for dating by the bulk-rock Rb-Sr isochrone method because of their low degree of differentiation and low variations of Rb/Sr ratios. The rocks also do not fit requirements of mineral isochrone dating, as it is impossible to separate the monomineral fractions from them because of their fine-grained structure. Therefore, the Hopunvaara intrusion, differentiated in composition from alkaline olivine dolerites to monzodiorites and quartz–monzonites and characterized by significant variations of Rb/Sr ratios from 0.10 to 0.33, was chosen for the investigations.

The Hopunvaara intrusion is a subvolcanic, stock-like body (evidently, neck) isometric in plan, of 550 × 750 m in size. The intrusion is located at the western exocontact of the rapakivi granites of the Salmi massif, amidst the metamorphic rocks of the Early Proterozoic Ladoga Group (Fig. 1). The geophysical and the drilling data revealed that at depth, the intrusion breaks through the rapakivi granites of the Salmi massif and associated tin-polymetallic scarn ores, whose age is 1550 ± 30 Ma, according to the data of Rb-Sr isochrone method (Schergina *et al.*, 1982), and 1546 ± 20 Ma, according to the Sm-Nd isochrone method (Amelin *et al.*, 1991; Larin *et al.*, 1992).

The rock composition varies from sub-alkaline olivine gabbro–diorite to quartz monzonite. Basaltic, trachybasaltic, and latitite porphyrites appear at the contact zones. Distinct lamination, pronounced in a subparallel alternation of zones, composed of rocks with different composition, is locally observed in the stock (Geologiya..., 1987). By their petrochemical features, the rocks of the Hopunvaara intrusion are practically identical to the rocks of the Valaam laminated sill. On the $(Na_2O + K_2O)$–SiO_2 diagram (Fig. 2), the rock data-points are exclusively localized in the field of subalkaline rock series. They are characterized by a rather high titanium content (TiO_2 = 1.24 - 4.20%, with an average value of 2.43%), a high iron content (K_F = 54.1 - 83.3, f = 17.3 - 24.7), a high alkalinity ($Na_2O + K_2O$ = 2.52 - 6.65%), with a rather significant proportion of potassium (Na_2O/K_2O = 0.37 - 2.45), a high content of P_2O_5 (0.42 - 0.96%), low content of aluminum (al' = 0.69 - 0.98) and magnesium (MgO = 1.43 - 9.50%, or 4.47% average). They resemble basalts of the Salmi locality in titanium and iron contents, elevated alkalinity, and low alumina and magnesia contents. However, the range of SiO_2 and alkali contents in the rocks of the Hopunvaara intrusion is much wider (Fig. 2), which seems to be, on the one hand, a result of contamination by more acid host rocks and, on the other, a consequence of the high differentiation of this small intrusion.

The Jotnian magmatic rocks of the North Ladoga region and Scandinavia are quite similar to the continental subalkaline basalts in their petrochemical features. On Pearce's diagram, (Fig. 3) most of the data points of these rocks plot in the field of the continental riftogenic basalts.

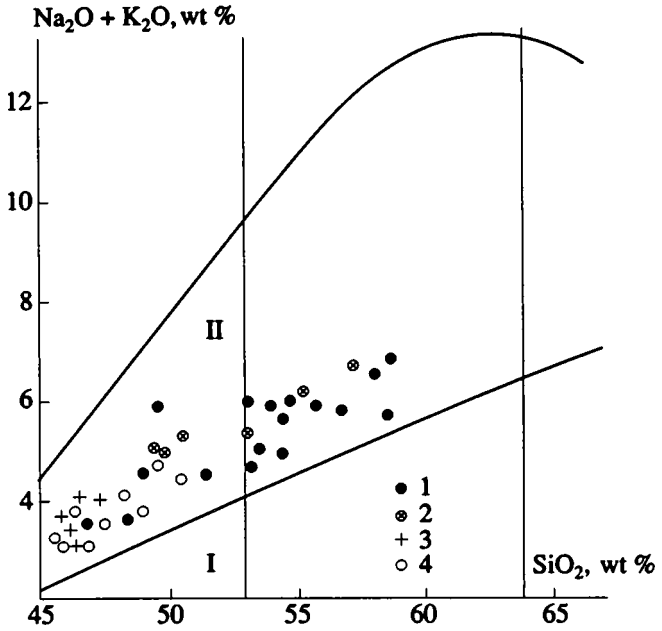

Fig. 2. *The composition of the Jotnian magmatic rocks of the southern part of the Baltic shield on the classification diagram ($Na_2O + K_2O$)–SiO_2.*

1 – the Hopunvaara intrusion; 2 – the Valaam sill; 3 – volcanites of the Salmi Formation; 4 – dikes and sills of the Satakunta basin. Fields of magmatic rocks: I – the normal series and II – the subalkaline series (Magmaticheskie Porody..., 1983).

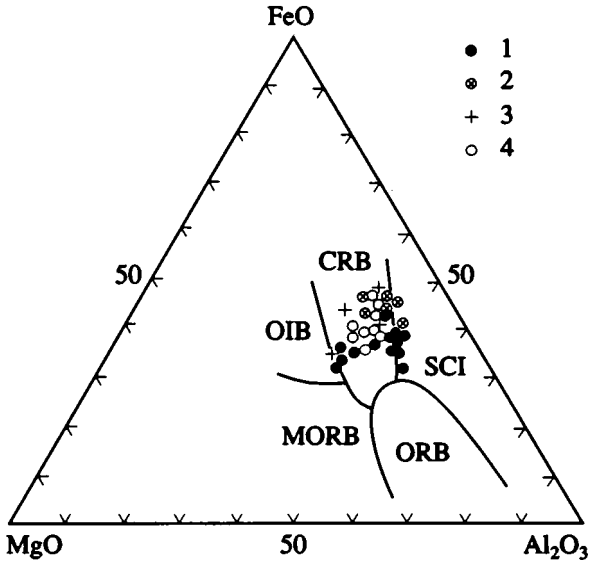

Fig. 3. *The composition of the Jotnian magmatic rocks of the southern part of the Baltic shield on the diagram MgO–FeO–Al_2O_3, T. Pearce (1977).*

1 – the Hopunvaara intrusion; 2 – the Valaam sill; 3 – volcanites of the Salmi Formation; 4 – dikes and sills of the Satakunta basin.

MORB – mid-ocean ridge basalts, OIB – oceanic islands basalts, CRB – continental rift basalts, ORB – island arc basalts, and SCI – basalts of the spreading center islands.

Five bulk samples of 7 - 10 kg each were selected from the borehole core for the Rb-Sr dating. The chemical composition of the studied rocks are given in Table 1. They are massive, fine to medium-grained, sometimes porphyritic rocks, varying in composition from quartz monzodiorite to quartz monzonite. The rock textures are hypidiomorphic, gabbro–ophitic, and poikilophitic. The main minerals are represented by idiomorphic, sometimes zonal plagioclase An_{55-60}, clinopyroxene (augite), and occassionally brown hornblende. Accessory minerals are orthopyroxene (hypersthene), titanomagnetite, apatite, potassium feldspar, and quartz. The latter two minerals commonly occur as a granophyre aggregate in the interstices or as segregations irregular in shape, more fine-grained than the groundmass. The potassium feldspar is strongly altered, and frequently has a metacolloidal and spherulitic structure.

The secondary autometasomatic alterations are weak and irregular, resulting in the sericitization and saussuritization of plagioclase, the actinolite and chlorite formation after the dark minerals, and the appearance of late brown-green biotite. The least altered autometasomatically are the rocks samples 689-15, 689-10, and 689-5.

The Rb and Sr contents and the Rb/Sr ratio in the studied samples were estimated using the X-ray spectral method by a VRA-30 analyzer. The element concentrations were analyzed with an accuracy of ±10%, and the analytical error of the Rb/Sr ratio determination, was ±1.5% (1σ). For estimation method see (Krylov, 1979).

The isotope composition of Sr, separated using the ion exchange column after the chemical decomposition

Table 1. Chemical composition of the Hopunvaara intrusion rocks

Sample number	Rock	SiO_2	TiO_2	Al_2O_3	$Fe_2O_3^*$	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5	L.O.I.
690-13	Quartz monzonite	58.50	1.89	12.88	12.45	0.14	1.43	4.55	3.17	3.48	0.53	0.50
689-36	»	55.35	2.23	13.93	12.28	0.13	1.96	5.40	3.67	2.77	0.71	1.07
689-5	»	54.90	2.24	14.85	11.58	0.14	3.66	5.58	3.00	2.41	0.51	0.64
689-10	»	54.31	2.45	14.60	12.43	0.15	3.74	5.96	3.00	1.86	0.54	0.50
689-10	Quartz monzodiorite	53.06	2.76	14.55	12.96	0.16	3.91	6.31	2.85	1.98	0.52	0.50

* *All iron is given as Fe_2O_3.*

Table 2. Rb-Sr analytical data for bulk rock samples of the Hopunvaara intrusion

Sample number	Content, ppm		$^{87}Rb/^{86}Sr$	$^{87}Sr/^{86}Sr$
	Rb	Sr		
690-13	86	256	0.9589	0.72514
689-36	77	349	0.6277	0.71855
689-5	59	451	0.3780	0.71391
689-10	38	367	0.3061	0.71242
689-15	45	445	0.2942	0.71263

of samples, was measured on a MI-1320 mass spectrometer. The measured $^{87}Sr/^{86}Sr$ ratio in the interlaboratory standard SRM-987 in the experimental period was 0.71021 ± 0.00005 (1σ). The analytical error of $^{87}Sr/^{86}Sr$ ratio determinations was estimated as ±0.05% (1σ). The age and the initial $^{87}Sr/^{86}Sr$ ratios were calculated using the least squared polynomial method (Shukolyukov *et al.*, 1974).

The Rb-Sr analytical data are given in Table 2 and graphically shown in Fig. 4. The straight line approximating the relationship between the $^{87}Sr/^{86}Sr$ and $^{87}Rb/^{86}Sr$ ratios in the studied samples is characterized by the root-mean-square ratio, equal to 0.33. This permits a consideration of it as an isochrone, giving an age of 1330 ± 50 Ma and an initial $^{87}Sr/^{86}Sr$ ratio equal to 0.7068 ± 0.0004 (the above errors correspond to one standard deviation).

The obtained age value is within the limits of determination error and coincides with the recent data on the K-Ar ages of the Salmi basalts published by R.A. Khazov (1973). Along with the spatial proximity and petrochemical similarity of both formations, the results support the idea of the comagmatic origin of the formations (Golubev and Svetov, 1983). The dating obtained is of great stratigraphic importance, as it provides a coherent age of the North Ladoga Jotnian rocks (the Salmi basalts and the Hopunvaara intrusion). Thus, the isotope age of the earliest Riphean formations in Karelia is about 1330 ± 50 Ma. In addition, it should be emphasized that the dating obtained indicates that the magmatic formations of the North Ladoga region belong to the first impulse of the Jotnian magmatism, synchronous to the processes of the sedimentogenesis in the Jotnian graben–synclines. The basic magmatism of that time was previously reported only from one area of the Baltic shield, in Central Sweden (dikes of Tuna dolerites). This magmatic impulse within the Svecokarelian region is coequal to the nonorogenic stage of the Gothian orogenic cycle in the contiguous Sveconorwegian folded belt.

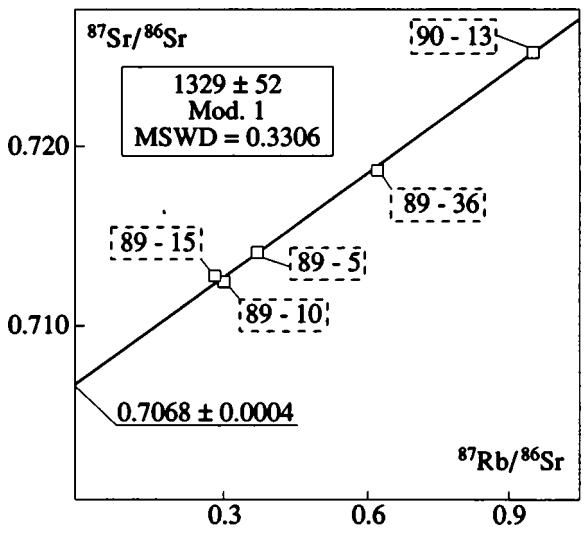

Fig. 4. *Bulk-rock Rb-Sr isochrone for quartz monzonites and quartz monzodiorites of the Hopunvaara intrusion.*

The processes of contamination by the material of sialic host rocks, which had a long crustal history, seem to be largely responsible for the elevated initial $^{87}Sr/^{86}Sr$ ratio (0.7068 ± 0.0004) in the rocks of the Hopunvaara intrusion, as compared to the less hybridized basic magmatic rocks of the Jotnian age in Sweden (0.703 - 0.7032). In general, the initial $^{87}Sr/^{86}Sr$ ratios in the non-contaminated Jotnian dolerites of the Baltic shield agree well with the values typical for intraplate basaltoids.

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Structure and Sedimentation Environments of the Riphean Bezymyannyi Formation in the Turukhansk Uplift, Siberia

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Abstract – The structure of the Bezymyannyi Formation, whose thick siliciclastic strata compose an apparent base of the Riphean in the Turukhansk uplift, has been considered. An analysis of rock structures and cyclic constitution of the sequence, together with the reconstructions of paleocurrents, suggests that sedimentation occurred at a shallow-water shelf with a storm regime. An open sea is supposed to be situated north–northwest of the area of investigation. The inner and outer shelf environments, separated by the transitional zone of energy dispersion, were identified within the Bezymyannyi basin. The change of environments in time has been shown too.

Lately, geologists have become more interested in the nature of Precambrian basins, attempting to reveal their specific features and to separate, in time and space, the facies (ecologic) and evolutionary components, which influenced the distribution of Precambrian fossils and organo-sedimentary structures.

Examples of a facies analysis of the upper Precambrian in Northern Eurasia can be found mainly in English publications (Johnson, 1977; Tucker, 1977; Levell, 1980; Fairchild, 1989). An almost singular exception in the Russian literature is the study of the Riphean in the Urals (Maslov, 1988). However, the conditions and environments of sedimentation have been considered in this work very generally, without going into required details.

This paper is aimed at the description of the structure and the reconstruction of the sedimentation environments of the Bezymyannyi Formation, whose thick siliciclastic strata compose an apparent base of the Riphean in the Turukhansk area. The Riphean section of the Turukhansk area, more than 4 km thick, is one of the reference sections in Siberia, and its regional stratigraphic scale, elaborated in the 1940s, was considerably changed only in its upper part (Komar and Serebryakov, 1969). However, the position of the Middle–Upper Riphean boundary in this section remains debatable (Semikhatov and Serebryakov, 1983; Khomentovskii *et al.*, 1985; Kozlov *et al.*, 1988; Komar, 1990). In this paper, this boundary is drawn at the base of the Derevnya Formation, as it is adopted in modern unified scales of the Siberian Riphean and substantiated in monograph of the Semikhatov and Serebryakov (1983).

Three blocks, elongated in a nearly north–south direction, bounded by reversed-overthrust faults, and displaced eastward to the Siberian craton margin, can be identified within the Turukhansk uplift. Riphean deposits within the blocks compose the monoclines gently dipping westward, and are overlain in some places by the gently dipping Vendian-Cambrian deposits.

The Bezymyannyi Formation crops out in two eastern monoclines, almost along its whole length: in the north, along the Kamennaya River (the left tributary of the Bol'shaya Shorikha River); in the central part, along the Nizhnyaya Tunguska River, within the Golyi Yar (in the east) and Turukhansk (in the west) monoclines; and in the south, along the Sukhaya Tunguska River (Fig. 1). In this paper I consider the structure, sedimentation conditions, and environments of the Bezymyannyi Formation, using the data on the four above-mentioned sections and developing the concepts outlined on the basis of the study of only the northern section (Petrov, 1993).

STRUCTURE OF THE SECTIONS AND LITHOLOGY OF THE BEZYMYANNYI FORMATION

The Bezymyannyi Formation is represented by an intricate intercalation of sandstones, siltstones, and claystones which is conformably overlain by clayey-carbonate rocks of the Linok Formation and bounded by reversed-overthrust faults at the base. I draw the formation upper boundary along the top of the last sandstone bed, somewhat lower than did previous investigators. It is this boundary that separates the terrigenous siliciclastic rocks from the clayey-carbonate strata of the Linok Formation that is conformably overlying them. The Linok Formation itself is represented by the rocks with different structural features (Petrov, 1993). This boundary is very distinctly pronounced in all sections of the Turukhansk uplift.

The Bezymyannyi Formation can be subdivided into three subformations. In its thickest section (up to

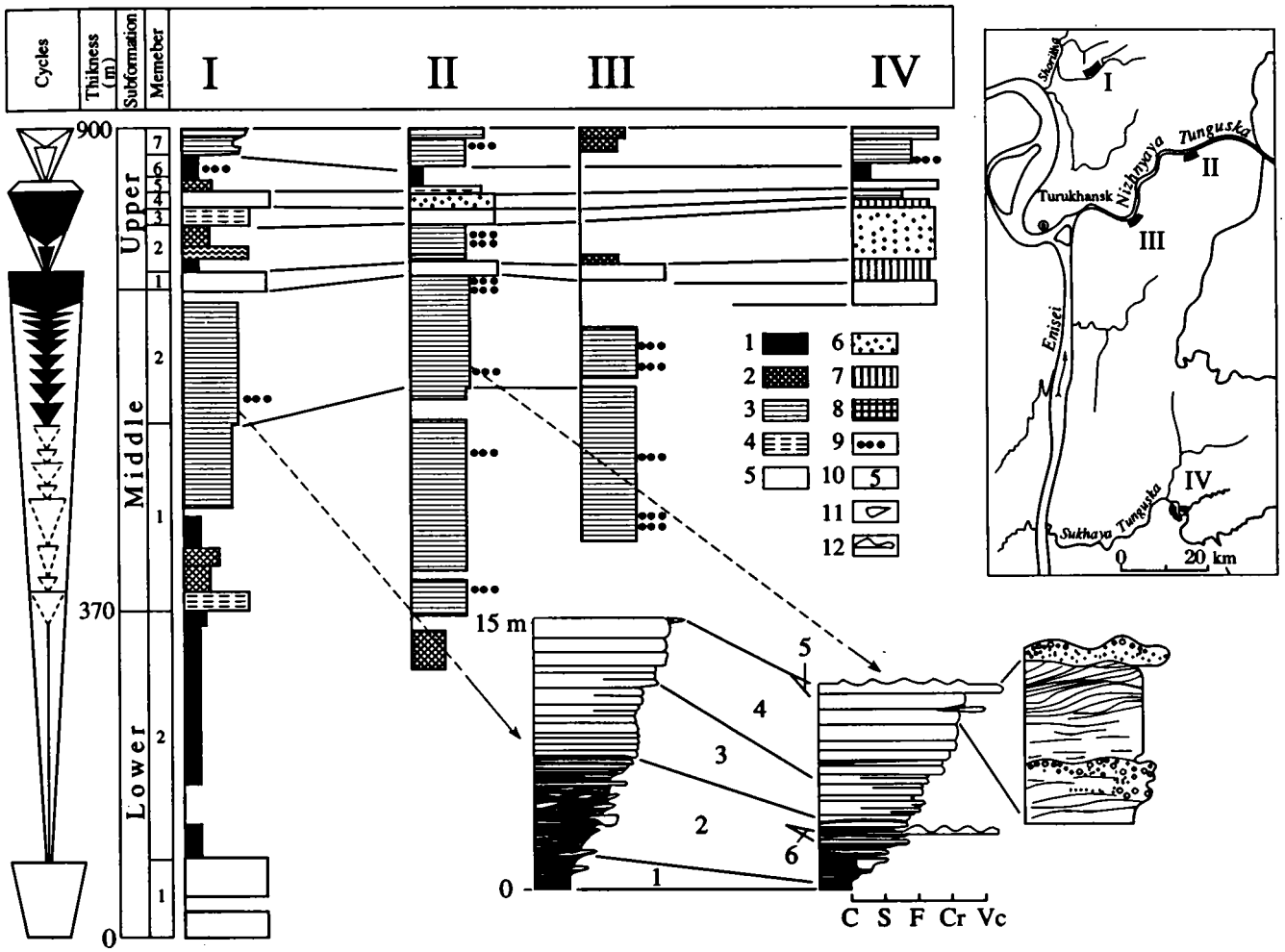

Fig. 1. *Schematics of the position and facies structure of the Bezymyannyi Formation sections.*

1 - 8 – facies associations: 1 – claystone–siltstone, 2 – claystone–siltstone–fine-grained sandstone, 3 – claystone siltstone–fine-grained sandstone–coarse-grained sandstone, 4 – fine-grained sandstone–coarse-grained sandstone –very coarse-grained sandstone, 5 – coarse-grained sandstone–very coarse-grained sandstone, 6 – coarse-grained sandstone–very coarse-grained sandstone–inequigranular sandstone, 7 – coarse-grained sandstone–fine-grained sandstone and claystone, 8 – coarse-gritstone– siltstone and fine-grained sandstone; 9 – granule sandstone facies; 10 – numbers of facies, composing a cycle (see text); 11 – erosional channels (gutter casts); 12 – ripple marks.

C – claystone, S – siltstone; sandstones: F – fine-grained, Cr – coarse-grained, Vc – very coarse-grained. The column width corresponds to the mean grain size of the rock material.

900 m), exposed along the Kamennaya River, the lower subformation with an apparent thickness of 370 m consists of two members, the lower composed of light-gray coarse-grained sandstone and the upper, of dark-gray mudstone with subordinate interbeds of fine-grained sandstone. The middle subformation, 350 m thick, consists of a clearly cyclic alternation of mudstone and sandstone. It can be tentatively subdivided into two members, with a clear cyclic character and a lesser share of fine-grained rocks in the upper one. The upper subformation, 180 m thick, is composed of various rocks, from claystones to coarse-grained sandstones, with an appreciable predominance of the latter. Of its seven members, the lower five exhibit a considerable facies variability, while members 6 and 7 are fairly persistent. The base of member 6 is very easily traceable throughout the area (Fig. 1).

Truncation of the Bezymyannyi Formation into various parts by the reversed-overthrust faults resulted in decreasing the stratigraphic range of its exposed rocks from the north southward. Its most complete section is situated in the Kamennaya River basin. Along the Nizhnyaya Tunguska River, a considerable part of the lower subformation is absent, and along the Sukhaya Tunguska River, only the upper subformation can be found in complete section (Fig. 1). Thus, the apparent thickness of the formation decreases from the north southward from 900 to 190 m. The middle subformation becomes appreciably thinner with the transition from the northern section to the sections of the central part of the area, and this is accompanied by an appreciable thinning of its cycles. However, the thickness of the middle subformation does not change in two sections of the central part of the area (the Golyi Yar and

Turukhansk monoclines along the Nizhnyaya Tunguska River), and thicknesses of its cycles there also remain unchanged; this corresponds to earlier conclusions concerning the persistence of the Bezymyannyi Formation beds in this part of the area (Ivanovskaya and Afanas'ev, 1970). The upper subformation is persistent in thickness in its central and southern sections, its thickness slightly increasing in the north at the expense of some swell of the two lower members (Fig. 1). As was already noted, the members of this subformation exhibit considerable facies variations. A noticeable variation in the lithology can also be observed in other intervals of the section. In a very general way, this can be expressed as an increase in the share of fine sediments (mud) northward. Another general tendency in the lithology change in the Bezymyannyi Formation is an increase upsection in the share of coarse clasts (medium- and coarse-grained sands).

The subarkosic character of the Bezymyannyi Formation sandstones and siltstones is persistent throughout the section; the content of quartz varies from 70 to 80%, and of plagioclase (oligoclase–andesine), from 10 to 20%. The amount of potassium feldspar is usually 1 - 5%. Sandstones contain clastic muscovite flakes confined to the finest fractions. The content of rock fragments (microquartzite) does not exceed 5%, and of heavy minerals, among which the most widespread are zircon, magnetite, and tourmaline, 0.1%. Characteristic of the sandstones is quartz overgrowth of quartz grains; less frequent is clayey cement (illite, chlorite) formed later. The small amount of pyrite in the sandstones is, apparently, formed even later than the clayey cement.

The clayey part of mudstones is represented by illite and iron-magnesian chlorite. The mudstones do not contain pyrite, though their content of disseminated organic matter reaches a few percent (Bazhenova *et al.*, 1970), suggesting a limited scale of sulfate reduction during diagenesis. Nevertheless, solitary small sphalerite (cleiophane) concretions have been found in the middle subformation mudstones in the Kamennaya River section.

The apatite segregations in mudstones and sandstones are confined to the sections of the central and southern parts of the Turukhansk area, being present with considerably less frequency in the north. Glauconite is rather widespread in the middle subformation siltstones and sandstones of the sections in the central part of the area (Nizhnyaya Tunguska River); in the north of the area its grains have been found only rarely in the coarse-grained sandstones.

THE BEZYMYANNYI FORMATION FACIES

In this paper, according to Gressly's classic definition, the term *facies* refers to the part of the section differing from the overlying and underlying rocks in a number of characteristic features; the facies are classified according to the rock type most widespread within it. Three facies groups have been identified in the Bezymyannyi Formation. The first group (facies 1 - 5) is most widespread, being present throughout the formation sequence and forming a close association. The second group is represented by a single, dearly subordinate facies 6, which is present sporadically, though throughout the sequence. The third group (facies 7 - 9) has been found exclusively in the upper subformation of the central and southern parts of the area, and is unknown in the north (Fig. 1).

(1) The claystone facies is represented by dark-gray and black claystones with an even plane lamination (laminae 0.1 - 1 mm thick) emphasized by variations in the distribution of silty and organic matter admixtures. Silt-size muscovite flakes prevail among the clastic components. Thin graded bedding is frequently present. Claystones compose thin (1 - 20 cm) layers the boundaries of which are sharp at the base and usually gradual at the top.

(2) The siltstone facies consists of dark-gray and greenish-gray claystone, siltstone, and very fine-grained sandstone with individual beds or, less frequently, lengthy lenses of dark-gray fine-grained sandstone, 0.5 - 10 cm thick. Characteristic of the fine-grained sandstone is a flat bedding emphasized by thin (ca. 0.1 mm) films of black clayey matter. Often the films occur in the upper parts of sandstone beds. A very gentle cross and cross-undulatory bedding, infrequently graded bedding, and erosional base are characteristic of the lenses. In the Nizhnyaya Tunguska sections, the facies rocks contain appreciable accumulations of glauconite.

The described rocks enclose casts of erosional channels or gutter casts (Whitaker, 1973), which are rather steep scours, 5 - 20 cm deep and up to 30 cm wide, filled with very fine-grained sandstone with a horizontal bedding or a very gentle cross-bedding dipping along the channel. The channels twist in a horizontal plane, with the outward sides of the bends being steeper than the inner ones, as in river meanders (Fig. 2). The channel walls are smooth or striated lengthwise; sometimes there are small second-order scours. The length of the channels is unknown, but in some of the smallest, a pinching out can be observed: the channel rapidly widens, becomes gentler, and disappears. The rocks of this facies form lithologically inhomogeneous layers, 2 to 10 m thick, and are connected by gradual transitions with underlying and overlying rocks.

(3) The fine-grained sandstone facies is composed of gray and dark-gray fine-grained sandstones with distinctly subordinate claystone and siltstone interbeds. The sandstone beds, 5 to 30 cm thick, separated by thin (0.5 - 2 mm) interbeds of black claystone, usually form packets, 0.5 - 3 m thick (Fig. 4). The bed surfaces are usually even, but sometimes, e. g., in the Golyi Yar monocline sections on the Nizhnyaya Tunguska River, have symmetrical ripple marks with a wave length of 6 to 30 cm. Rather frequently, polygonal structures similar to the Rhysonetron structures (Hofmann, 1971) can be seen on bedding surfaces. The polygonal systems formed by elongated sandstone bodies are elliptical in cross section and measure from 1 to 5 mm across.

Fig. 2. *An isolated erosional channel (gutter cast) in sandy-clayey rocks of the siltstone facies. Two conjugated meanders of the channel can be seen. The graduated scale in the upper part of the figure is 4 cm long.*

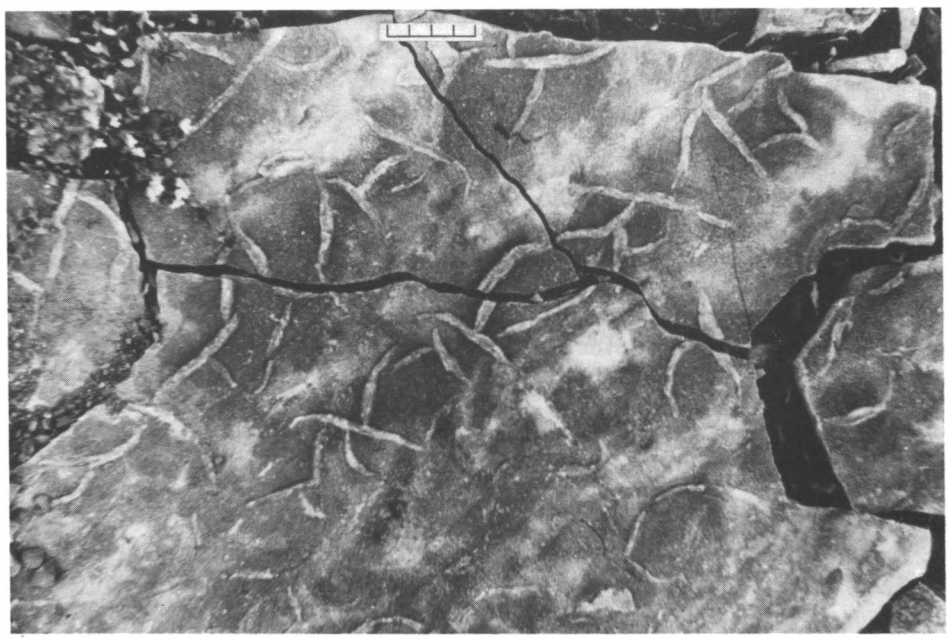

Fig. 3. *A Rhysonetron structure on the top of a fine-grained sandstone bed. Crack systems stretch along the ripple troughs. The graduated scale in the upper part of the figure is 4 cm long.*

They are situated inside claystone interbeds, and distributed evenly on bedding surfaces or stretched along the ripple scours (Fig. 3). Characteristic of the sandstones, in most cases, is a horizontal or gently dipping wavy bedding; a small-scale cross-undulatory bedding can be infrequently observed. The bedding is marked by thin (ca. 0.1 mm) black films of clayey matter; detritus of these films and of claystone laminae, 1 mm to 4 cm thick, is also often present. Fine granulometric sorting is characteristic of sandstone microstructures. Sandstones from the Nizhnyaya Tunguska sections contain glauconite. Rocks of this facies compose layers a few meters thick and have gradual transitions to the rocks of other facies.

Fig. 4. *Sandstone facies: 3 – fine-grained and 4 – coarse-grained.* The apparent thickness of the outcrop is 2.5 m.

(4) The coarse-grained sandstone facies consists of light-gray medium- and coarse-grained sandstones, usually composing thick (20 to 60 cm) beds. Characteristic of the lower parts of the beds are massive, thick horizontal, or flat-wavy bedding, and of the upper parts, crosswary bedding with large asymmetric ripple marks of an amplitude up to 30 cm. The hummocky cross-stratification (Dott and Bourgeois, 1982) is present rather seldom. In some cases, large unidirectional cross-bedded layers without clear oscillations can be observed, but the angles of their foresets are extremely variable, from 10° to 60°. The grains of sandstones are well reworked and rolled. The packets of sandstone beds, from three to several tens of meters thick, are very persistent along the strike, for hundreds of meters. Sometimes thin-bedded (up to 10 cm) sandstones of darker color, containing fragments of thin claystone laminae, are present at the base of such sets. In some cases, lenses of black claystone, 1 - 5 cm thick, are present between the sandstone beds. This claystone sometimes contains apatite segregations, and the sandstone includes fragments of phosphate concretions. Scattered glauconite grains are often present in the sandstones. Solitary load casts can be observed at the tops of the beds.

(5) The very coarse-grained sandstone facies is represented by light-gray coarse- and very coarse-grain- ed sandstones, sometimes containing scattered granule-size grains. Large symmetric ripple marks with a wave-length of up to 50 cm are often present at the tops of the beds. The coarsest fractions are present at the ripple crests, and glauconite grains sometimes concentrate in the ripple scours. The granule-size fraction in some cases contains fragments of the enclosing sandstone with phosphate cement. On the whole, the granule-sandy deposits are poorly sorted and have an unclear horizontal wavy bedding. The rocks compose individual interbeds, up to 30 cm thick, among the rocks of the coarse-grained sandstone facies. These interbeds have either sharp boundaries or gradual transitions to underlying rocks.

As was already noted, the above five facies are most widespread in the Bezymyannyi Formation. They form strictly repeating successions (associations) which will be considered below. The following facies are of limited distribution in the sequence.

(6) The gritstone facies is composed of dark-gray coarse- and very coarse-grained sandstones, poorly sorted, with an unclear horizontal wavy bedding. Often gravel-size grains, pudding gravestones, and a considerable admixture of silty material are present in the sandstones. The gravel-size grains are sometimes coated with black claystone films. The sandstones compose individual beds, 4 - 15 cm thick, with sharp boundaries. Large symmetric ripple marks (wavelengths up to 40 cm) can be often observed at the tops of the beds. Such beds are mainly confined to the siltstone facies.

(7) The inequigranular sandstone facies is represented by light-gray and gray sandstones, usually medium- and fine-grained, but often of a wide granulometric spectrum and, as a result, with the grain size varying within individual laminae from fine to very coarse sand and occasionally to fine gravels. A rapid grain-size change can be observed both in the vertical sections of individual beds and laterally. Residual flaserlike thin (0.5 - 5 mm) fragments of mudstone are often present inside the beds, and scattered fragments of a sandstone with phosphate cement, up to 5 mm across, are present among the very coarse fractions. The sandstones have a

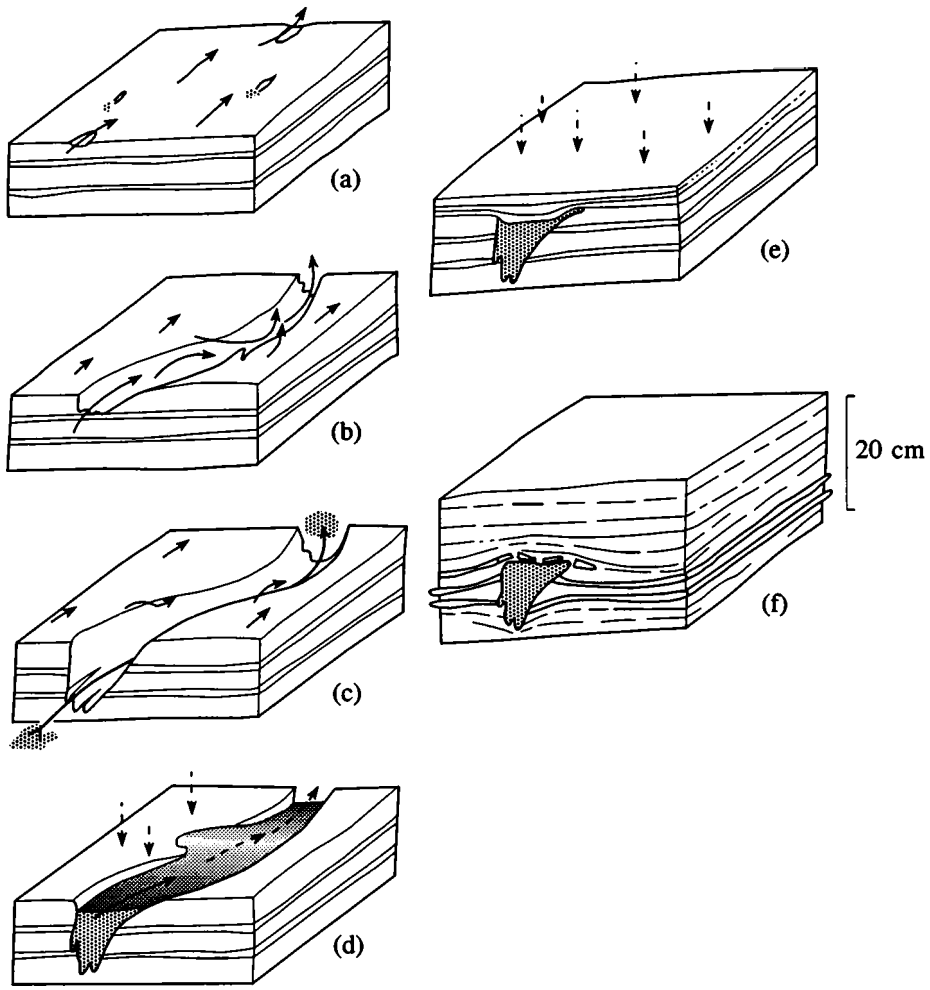

Fig. 5. *Model of the supposed formation of an isolated sand fill of an erosional channel (gutter cast).*
(a) Initial stage: fluctuations of a weak natural flow, shallow scours on the surface; (b) Early stage: initiation of meanders and rapid channel deepening. Increase of flow velocities inside the channel and their decrease at the sediment surface; (c) mature stage: a formed channel. Maximum difference of the flow velocities inside the channel and at the sediment surface; (d) concluding stage: general decrease of the flow velocities. Filling of the channel with fine-grained sand; (e) burial of the channel. Calm-water sedimentation; (f) a present-day appearance of the sandstone fill. Bed deformation resulted from the sediment diagenetic compaction.

small-scale (3 - 10 cm) cross-wavy bedding and compose beds of variable thickness (mainly 3 to 15 cm) with sharp, often erosional boundaries within the coarse-grained sandstone facies.

8. The fine-grained sandstone and claystone facies is an alternation of dark-gray sandstones, often composing lenses up to 3 cm thick, and black claystone interbeds, ca. 1 mm thick. A very gently dipping cross-bedding marked by flaserlike fragments of clayey matter drapes is characteristic of the sandstone lenses. The rocks of the facies compose two members, up to 20 m thick, in the southern section of the formation (Sukhaya Tunguska River).

9. The siltstone and fine-grained sandstone facies is an interlamination of light-gray fine-grained horizontally laminated sandstones and dark-gray siltstones, an 1 - 2 cm thick, with black claystone interbeds, 1 - 4 mm thick, and subordinate beds of dark-gray horizontally bedded fine-grained sandstones, containing small, up to 2 cm across, claystone fragments. Structures of the Rhysonetron type are abundant in the rocks, and their condensation results in the appearance of characteristic nodular-vermiform structures. The rocks of this facies, along with those of the coarse-grained sandstone facies, compose a rather homogeneous member, 15 m thick in the Sukhaya Tunguska section (Fig. 1).

SEDIMENTATION CONDITIONS AND ENVIRONMENTS

The five most widespread facies of the first group compose, in order of their description, strictly repeated successions, which have the features of the upward shallowing cycle indicated by the monotonously increasing grain size upsection (Fig. 1) while sandstone beds become more flaggy (Fig. 4). Often certain cycles lack the very coarse-grained sandstone facies. In some cases, the section also lacks coarse-grained and, occasionally, fine-grained sandstone facies; however, such a reduced cycle does not lose its upward shallowing char-

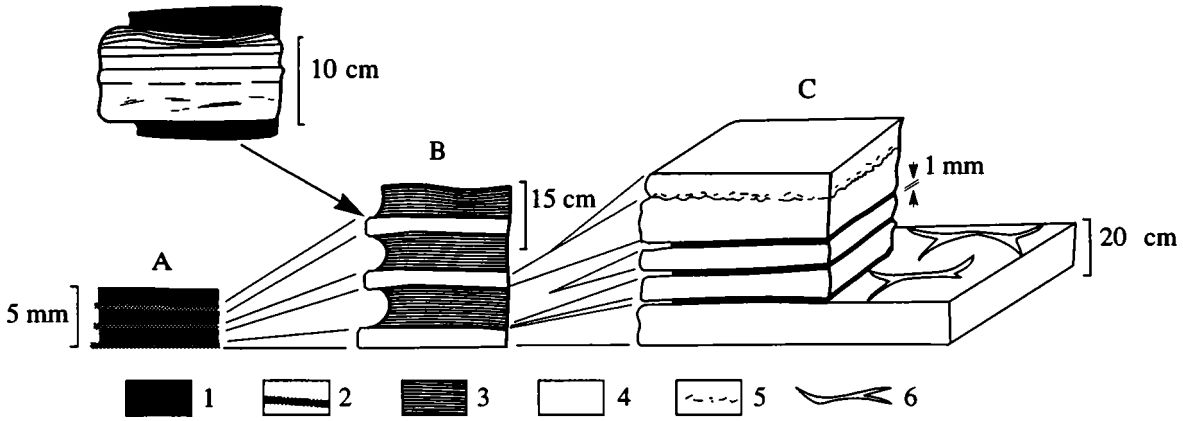

Fig. 6. *Assumed rock interrelations in the facies.*
A – claystone, B – siltstone, and C – fine-grained sandstone. 1 – claystone; 2 – fine siltstone; 3 – mudstone; 4 – fine-grained sandstone; 5 – small fragments of claystone laminae; 6 – Rhysonetron structures.

acter. An instance of the complete cycle, considered below, noted that facies inside a cycle are connected by continuous transitions, and their boundaries must often be drawn rather tentatively, which suggesting a continuous change of sedimentation conditions. Proceeding from this suggestion and from the typical rock structures, the sedimentation conditions and their changes during the cycle formation will be considered below.

The claystone facies, composing the cycle base and having a sharp lower boundary, was formed by a slow deposition of clayey particles under calm-water conditions, only occasionally being disturbed by an invasion of small amounts of silt, forming microlaminae. The calmwater environment was not changed by such periodical injections, a conclusion that is suggested by the absence of washouts or any marks in the flat bedding. When the siltstone facies overlying the claystone was formed, the above conditions were disturbed by the deposition of more considerable amounts of very small-grained and fine-grained sands, sufficient for the formation of independent sandstone beds. There were some gaps in their deposition, which are marked by thin films of clay. An even horizontal bedding within an entire sandstone bed suggests sand sedimentation from suspensions, under calm-water conditions near the bottom, and hence turbulent flows transporting sediments in the water layer above. Such flows are characteristic of the basins with a storm regime of sedimentation (Aigner, 1985) and are well known in present-day seas. Side by side with the above structures of the facies there are small local washouts and a very gently dipping cross-bedding in the sandstones, resulting mainly from the activity of unidirectional weak flows near the bottom.

Isolated casts of erosional channels (gutter casts) in the rocks of the facies (Fig. 2) contribute to the interpretation of the sedimentation conditions of the facies. The steep sides of the scours suggest that those sediments already lithified, were eroded. The absence of large fragments inside the channels, and traces of erosion of the channel walls indicate that the eroding flows could transport only fine material. It is significant that the channels were formed under subaqueous conditions, as no traces of sediment desiccation can be observed at synchronous levels and, even more unusual, there were also no appreciable washouts. Such a differential erosion can be explained by the presence of local streamlike flows, creeping on the basin floor; an explanation that is generally in agreement with the observed channel meandering. I suppose that flows of rather high velocities sufficient for downcutting originated from a rather weak sheet flow near the bottom. In this case, extremely small erosional depressions of the floor were favorable for concentrating the flows near the bottom and for subsequent deepening of the scour with a simultaneous drop in the flow velocity at the sediment surface. The evolved channel system seems to be maintained for fairly long time spans, and the channels could be filled only after the extinction of the existing current system (Fig. 5). The gutter casts are characteristic features of some sediments of the tempestite group (Aigner, 1985).

Horizontally bedded rocks of the fine-grained sandstone facies, composing stratigraphically higher layers of the cycles under consideration, were formed under conditions resembling the described above, but the amount of sand deposited during a single event was greater than in the previous facies, as is reflected in the greater thicknesses of sandstone beds.

Continuous transitions between the three above considered facies in the cycle section imply certain spatial interrelations of these facies (Fig. 6). The trend in differences of the relative amount of sand observed in them seems to result from the dispersion and loss of sedimentary material as it moved away from the sources. This resulted in the thinning of sandstone beds, each corresponding to a single storm event. Probable gaps in sand delivery related to the fluctuations in flow velocities should be most clearly seen in the distal parts of the sedimentation area. This assumption is in agreement with the presence of thin clayey films in the sandstone beds of the siltstone facies. The Rhysonetron structures, confined to the fine-grained sandstone facies, seem to have been formed at an initial diagenesis stage (syneresis).

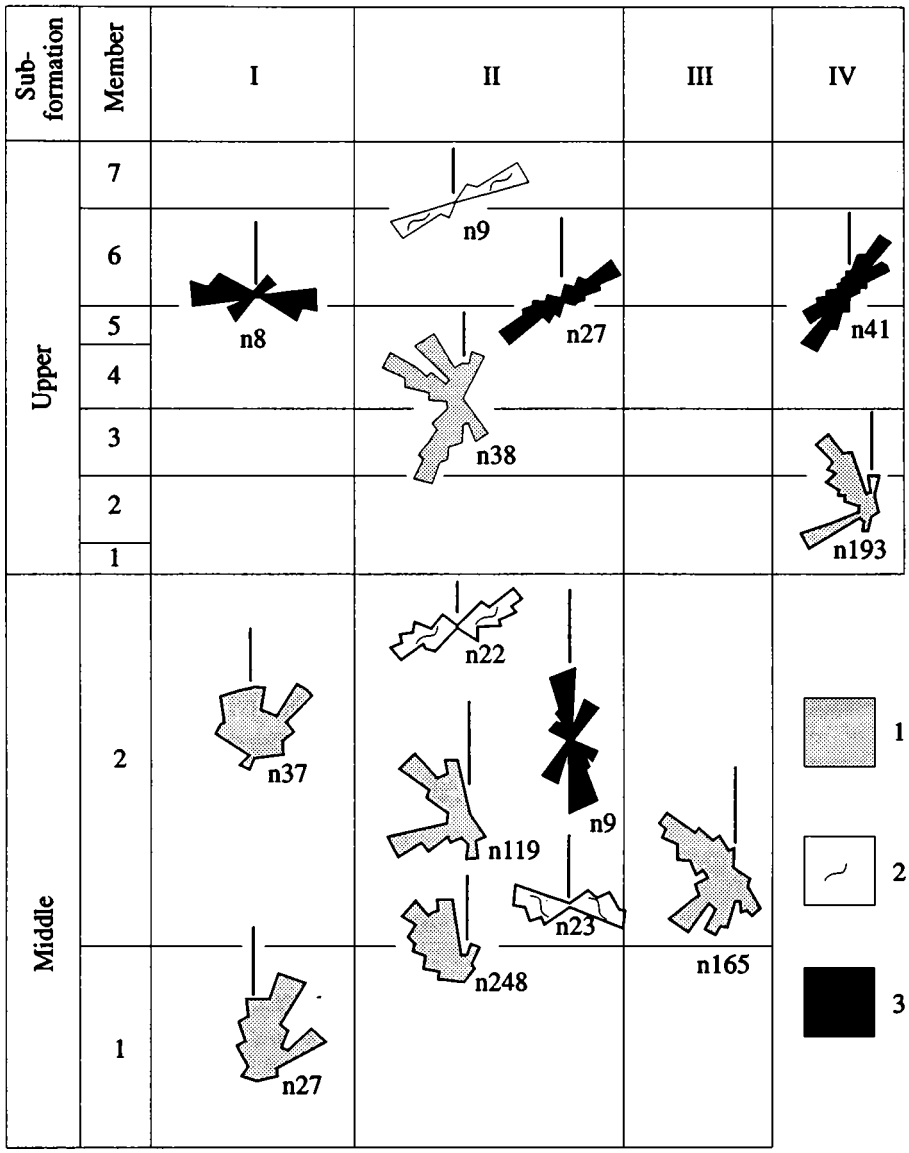

Fig. 7. *Data for reconstructing the Bezymyannyi basin paleocurrents.*
1 – foreset dips in the coarse-grained sandstone facies; 2 – orientation of ripple crests; 3 – strikes of erosional channels. I, II, III, and IV – positions of the sections (see Fig. 1): from the left to the right is from the north southward. Directions are given relative to the present-day geographic coordinate system being reduced to a common north-south line of the strike of the Turukhansk uplift structure.

This is indicated by a rather narrow interval of thicknesses (0.5 - 1 mm), of claystone laminae containing them, which can be explained by the influence of the load of rapidly deposited sand beds. However, the data available do not rule out the possibility of crack formation under subaqueous conditions (Plummer and Gostin, 1981; Kidder, 1990).

The sediments of the coarse-grained sandstone facies, occurring in the upper parts of the cycle, were deposited by means of high-velocity currents with the appreciable role of oscillatory wave movements. The above noted vertical succession of structures (Fig. 1) is a rather common phenomenon in such sediments and is usually interpreted as a result of different stages of a single sedimentation process (event). Thus, a coarse flat bedding at the base of the beds corresponds to the first, most active phase of this event, and a cross-wavy bedding of large asymmetric ripples in the upper parts of the beds corresponds to the combined flows of a comparatively lesser energy (Nottvedt and Kreisa, 1987; Mirow and Southard, 1991). The hummocky cross-stratification, noticeably less frequent in coarse-grained sandstones, suggests a limited influence of purely wave processes. Such successions are characteristic of tempestites forming in basin proximal zones and are well known in both older and present-day deposits (Kreisa, 1981; Dott and Bourgeois, 1982).

The rocks of the very coarse-grained sandstone facies, found at the tops of some beds of the coarse-grained sandstone facies, were formed as a result of the

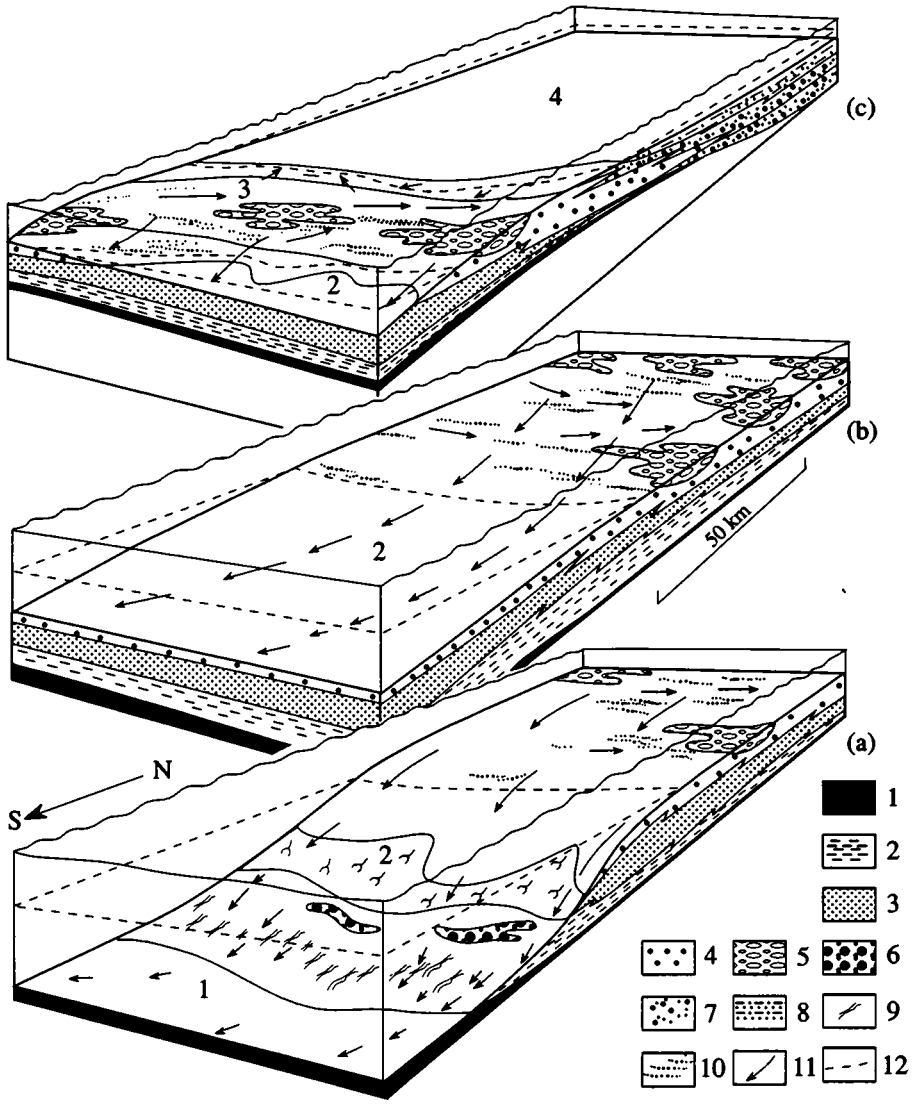

Fig. 8. *Sedimentation environments in the Bezymyannyi basin.*
(a) and (b) for sedimentation of the lower and middle subformations, (a) during the period of the maximum progradation rate (middle part of the cycle), (b) during the maximum shallowing upward (concluding stage of the cycle formation), (c) for sedimentation of member 4 of the upper subformation.

1 - 6 – facies: 1 – claystone, 2 – siltstone, 3 – fine-grained sandstone, 4 – coarse-grained sandstone, 5 – very coarse-grained sandstone, and 6 – gritstone; 7, 8 – facies associations: 7 – coarse-grained sandstone–inequigranular sandstone and 8 – fine-grained sandstone and claystone–siltstone and fine-grained sandstone; 9 – erosional channels; 10 – large ripples, 11 – current directions; 12 – storm wave base. Numerals in the figure: 1 – distal part of the outer shelf; 2 – proximal part of the outer shelf; 3 – zone of energy dispersion; 4 – inner shelf.

longer reworking of sediments by waves and currents, and may be considered lag deposits (Levell, 1980; Leckie, 1988). The very coarse-grained sandstone facies appears against the background of a general increase of grain size at the tops of some beds, composing the uppermost parts of the cycle (Fig. 1). This may be related both to the further growth of the environment energy and to the decrease of the amount of sediment delivered to the area on retention of the previous hydrodynamic regime. The large symmetric ripple marks inherent in this facies are evidence in favor of the above-hypothesis. Under such conditions finer fractions are removed, and fields of sandy-gravel deposits are formed, preserving the underlying sands from removal.

The two clearly pronounced parts of the considered cycle correspond to the two sedimentation zones of a basin different in environmental energy: a calm-water zone (the lower parts of the cycle represented by the claystone facies, siltstone facies, and fine-grained sandstone facies) and a high-energy zone (the upper parts of the cycle composed of the coarse-grained sandstone facies). The boundary between these zones corresponds to an abrupt change in energy, and approximately coincides with the storm wave base. In a cycle section, this

type of boundary is rather sharp, but usually not erosional, and this seems to be related to the character of a vertical distribution of the velocities of the storm gradient currents offshore.

Thus, the above described facies succession can be understood as a result of a storm progradation, characteristic of many tempestites, including Precambrian ones (Soegaard and Eriksson, 1985; Harris and Eriksson, 1990; Jackson *et al.*, 1990). The described sedimentation regime was characteristic of the middle Bezymyannyi Subformation, being particularly persistent during the accumulation of its upper member (Fig. 1). Note that the mean thickness of the ten cycles of this upper member increases from 10 m in the north to 15 m in the central part of the area. The thickness grows at the expense of finest facies, whereas the mean thickness of the coarse-grained sandstone facies decreases only very slightly (from 5 to 4 m, Fig. 1). Therefore, the more intense subsidence of the basin floor in the north and the greater depths of this part of the basin can be assumed. The main direction of foreset dips in the coarse-grained sandstone facies, indicating the sediment movement in the basin. The orientation of symmetric ripples in the very coarse-grained sandstone facies, extending parallel to the isobaths (Fig. 7), are in good agreement with this type of outline. Measurement of cross-bedding in the coarse-grained sandstone facies shows two directions of paleocurrents in the most proximal parts of the basin: the main north-northwesterly current and the southwesterly current perpendicular to it. The latter have been revealed only in the central sections, and was absent in the north. Thus, the two currents prevailed in the basin: the main current, transporting sediments north-northwestward by means of storm gradient flows deep into the basin, and the secondary current, flowing southwesterly, approximately parallel to the isobaths. It should be noted that in the northern section of the most open parts of the basin the main current deviated more in a northward direction. The almost north-south trend of erosional channels (gutter casts) in the upper member of the middle subformation implies that they were formed by offshore gradient currents in a more distal part of the basin, which corresponds to the general outline of paleocurrents.

The minimum depths of the basin under consideration could not be less than the thicknesses of the considered cycles. This type of approach to the estimation of paleodepths is used for deltaic cyclothems, although it does not take into account the rate of the floor subsidence and the effect of sediment compaction. However, it is quite evident that at the cycle end, a water layer had to be present above the sediment surface. The hummocky cross-stratification, characteristic of the coarse-grained sandstone facies and indicative of a storm wave base (Dott and Bourgeois, 1982), and the wavelength of symmetric ripple marks (Komar, 1974; Miller and Komar, 1980; Diem, 1985) make it possible to estimate the water depth at the time of cyclic accumulation of the middle subformation as a few tens of meters.

Coming to the gritstone facies, one should recall that it composes individual beds among the siltstone facies, occurring only occasionally in the cycle lower parts and standing out against the background of enclosing rocks for its rudaceous character (Fig. 1). The poor sorting of sand-size fractions and the invariable presence in them of a clayey-silty admixture, giving a dark coloring to the rocks, are characteristic features of this facies. The rudaceous character of sandstones and the large symmetric ripple at their bed tops suggest high-velocity long-period wave currents dominating during their accumulation, while the clayey-silty admixture suggests the temporary incostancy (episodic character) of such currents. Note that the sharp boundaries of this facies never are the first-order limitations, i.e., the boundaries of the cycles. This suggests that the gritstone facies is distributed locally, as can be illustrated by numerous sandy-granvel patches on the shelves of present-day seas (Leckie, 1988). Though many authors regard the formation of such sandy-granvel patches among fine sediments of an open shelf as a result of the activity of long-period waves, thus implying a storm regime of sedimentation, it is not yet quite clear what phenomena caused their appearance. Apparently, the gritstone facies was formed in some local zones of the basin with more intense hydrodynamics. This assumption results from the fact that the rock position of this facies cannot be correlated between the sections. It is interesting that the coarsest sandstones are present at two discrete levels: the gritstone facies at the lower level and the very coarse-grained sandstone facies at the upper. In present-day environments resembling the assumed above, the coarsest deposits are also found at two different depths (Shipp, 1984; Leckie, 1988), which are close to those assumed for the gritstone and very coarse-grained sandstone facies of the Bezymyannyi Formation.

The model of sedimentation environments for the accumulation time of the middle Bezymyannyi Subformation was constructed on the basis of the above data (Fig. 8). A wide migration of facies belts, reflected in cycles, was a decisive feature of that time. An analogous model would be applicable to the lower Bezymyannyi Subformation, taking into account its displacement into more distal parts of the basin, where the cyclic structure of the sections was lost, and to members 6 and 7 of the upper Bezymyannyi Subformation.

The other facies group, including the inequigranular sandstone facies, the fine-grained sandstone and claystone facies, and the siltstone and fine-grained sandstone facies, is present only in the upper Bezymyannyi Subformation (members 1 - 5). The inequigranular sandstone facies reflects conditions of lower energy than those of the coarse-grained sandstone facies closely associated with it. This can be inferred from both the smaller grain size of the sandy fraction of this facies and the lower amplitudes of its cross-wavy structures. The analysis of sedimentary structures implies that the sands were deposited under the influence of combined (wave and unidirectional) flows, and that the

grain-size variations seem to indicate that the velocities of these flows change in time. A considerable dispersion of their directions is indicated by a wide variation of foreset dip directions. Thin clayey flaserlike laminae in sandstones, which are present only in the Sukhaya Tunguska section, suggest periods of short-term calm, when the clayey material could be deposited.

The fine-grained sandstone and claystone facies and the siltstone and fine-grained sandstone facies were deposited under conditions of even lower energy of environment, which directly follows from their finer grain size. The bulk of sandy material in the latter of these two facies was deposited from suspensions into a muddy sediment, with no active currents near the basin floor. This is indicated by the plane lamination of the rock, the absence of washouts, and the usually observed gradual transition at the base of sandy laminae. These features bring the sediments of these two facies, in their formation conditions, together with the fine sediments of the lower parts of the above-considered cycles. However, no general trends in grain-size changes can be observed along the vertical section of the rocks composing these facies. The facies interrelations in members 1 - 5 of the upper subformation (Fig. 1) and the main directions of sediment transportation (Fig. 8) suggest that the above-mentioned facies were formed in the inner parts of the basin, sheltered from large storm waves coming from the north. This implies that the barrier dispersing wave energy was represented by extensive fields of coarse-grained and very coarse-grained sands, a few tens of kilometers wide. The sediments were transported, as usual, northwesterly, into the basin, and southwesterly, approximately along the isobaths; however, the foreset dip in the coarse-grained sandstone facies of members 3 and 4 suggests that the flow directions were deflected more to the south (Fig. 7). Thus, the storm waves penetrated into the basin inner zone for an appreciably less distance, and comparatively small amounts of sandy suspension were transported basinward by storm gradient currents. Such a situation, characteristic of members 1 - 5 of the upper subformation, was apparently caused by the subsidence rate slowing down together with the basin floor leveling, the sediment delivery decreasing, and a considerable amount of the coarsest sand concentrating in the remoter parts of the basin. The model of sedimentation environments for members 1 - 5 of the upper Bezymyannyi Subformation is shown in Fig. 8c. The deposition of these members, like those of the middle subformation, was marked by a wide migration of facies zones, which occurred in comparatively more proximal and shallow environments, and under conditions of a more leveled bottom topography, as is shown by the thicknesses of these intervals of the sequence. Three types of environments can be recognized within the shelf of this time: sheltered zones of the inner shelf, transitional zones of energy dispersion (barriers), and outer zones of the open basin.

CONCLUSION

The above data suggest that the Bezymyannyi Formation terrigenous deposits have been formed on a rather shallow shelf with a storm sedimentation regime. An extensive open sea basin was situated north-northwest of the sections under consideration. Waves from this basin influenced the whole sedimentation process; this influence was pronounced in sedimentary structures and in the directions of sediment transportation and wave propagation. A series of environments can be identified within the Bezymyannyi shelf: an inner shelf represented, apparently, by its distal part, a transitional zone of energy dispersion, separating the open basin from the sheltered zones of the inner shelf, and an outer shelf whose proximal and distal parts can be outlined (Fig. 8). No traces of the shoreline have been found in the sections of the Turukhansk uplift, but, judging from the position of isobaths reconstructed according to the orientation of large ripples, the directions of main paleoflows in the basin, and from the change of thicknesses, the coast was situated south and east of the area under study.

The above listed sedimentation environments changed during the basin evolution as a result of the migration of facies zones in the course of the general development of the basin. Analyzing the cyclic character of the Bezymyannyi deposits, it can be seen that in the Bezymyannyi Formation there are regressive cycles of two orders (Fig. 1).

The small-scale cycles, 10 - 20 m thick, described above in detail, could be caused by rather rapid sea-level oscillations within ten meters, with the migration range of facies zones amounting to only a few tens of kilometers. The short-term cycles were not observable in the most distal and deepest parts of the basin (the upper member of the lower subformation in the Kamennaya River section), while in the most proximal parts of the outer shelf and in the transitional zone their traces have been eroded. Therefore, the clearly cyclic character of the outer shelf sequence can be observed only in its individual intervals (Fig. 1). Within the inner shelf, the short-term cycles are reflected in the alternation of the coarse-grained sandstone facies and the siltstone and fine-grained sandstone facies (member 4 of the upper subformation in the Sukhaya Tunguska section). Coarse-grained sands accumulated during the periods of higher sea level, when the inner shelf was a transit zone, across which considerable amounts of sand migrated into the open basin. The fine sediments of the inner shelf were deposited during the periods of lower sea level, when the inner shelf was isolated from the open basin. It should be noted that such short-term cycles (10^4 - 10^5 years) are well pronounced in many Precambrian deposits resembling the Bezymyannyi ones (Soegaard and Eriksson, 1985; Harris and Eriksson, 1990; Jackson *et al.*, 1990) and to a lesser extent are characteristic of Early Paleozoic siliciclastic strata. A Rhysonetron structure, typical of many Proterozoic sequences (Hofmann, 1971; Kidder, 1990), also suggests the resemblance of basinal sedimentation conditions of siliciclastic sediments.

Characteristic of the large-scale shallowing-upward cycles that can be identified in the Bezymyannyi Formation sequence are their considerable thicknesses, and a general tendency to an increasing proportion of very coarse sand fractions upsection. Three such complete cycles can be identified in the entire sequence of the Bezymyannyi Formation with thicknesses of 650, 90, and 70 m from the base upward (Fig. 1). They have risen, probably, in relation to changes in the rate of basin floor subsidence, resulting in the lateral migrations of facies zones for many tens of kilometers (Fig. 8). During the formation of each of the three large-scale cycles, this migration occurred on the shelf with various bottom topographies, becoming in time less and less differentiated. The leveling of the basin floor, in turn, resulted in the extension of the facies zones. Thus, at the beginning of the third cycle (the base of member 6), the sea transgression resulted in the distal part of the outer shelf spreading through the entire known area of the Bezymyannyi basin. The extension of facies zones indicates a successively growing transgression of the Bezymyannyi sea; it should be noted that the main features of facies zones retained during the accumulation of the entire sequence of formation, and the depths of the basin, judging from the sedimentary structures, never exceeded the maximum depths of the early Bezymyannyi basin. Thus, the sequence of the Bezymyannyi Formation is in general the transgressive succession. Information on its earliest stage (member 1 of the lower subformation) is extremely scant due to the local distribution and poor exposure of this member; it can be, however, assumed that it is an uppermost part of a large-scale cycle, similar to those described above.

Storms generated two main currents within the proximal part of the outer shelf. A north-northwesterly ebb current, directed toward the open basin, left a very noticeable trace in the coarse-grained sandstone facies, where the foreset dips are oriented approximately across the strike of wave-ripple crests (Fig. 7). The second, west-southwesterly shoreline current, directed approximately along the ripple crests and, therefore, along the basin isobaths, may have resulted from the waves coming in obliquely with respect to the strike of the shelf topographic features. The current directions in the distal part of the outer shelf can be inferred only according to the orientation of erosional channels (Gutter casts) and, very rarely, to the cross-bedding of sediment filling them. Despite the limited information, certain tendencies in the distribution of paleocurrents in the shelf distal zones can be outlined. In the comparatively more proximal parts of these zones (middle subformation), the orientation of erosional channels coincides with the direction of ebb currents, and the foreset beds dip northward, while in the remoter parts (member 6 of the upper subformation) traces of easterly and northeasterly currents can be observed. The deflection of flows to the right with their movement basinward is distinctly pronounced in member 6 (Fig. 7). The deflection of ebb currents to the right can also be observed in the proximal part of the outer shelf (the coarse-grained sandstone facies in the middle subformation). This system of Bezymyannyi basin paleocurrents is shown in Figure 8. The deflections of the offshore gradient currents may be assumed to be caused by the Coriolis force, as the deflection magnitude (angle) depends directly on the distance passed by the flow in the basin. In this case, the Bezymyannyi basin was situated in the Northern Hemisphere.

The zones of the Bezymyannyi basin were not only pronounced in the rock facies, but also determined the distribution of organic-walled microfossils. Together with A.F. Veis, I have shown that the richest assemblages of these microfossils, including the morphotypes of intricate structure and maximum size, were limited in their lateral distribution by the proximal zones of the outer shelf (Ekosistemnye Perestroiki..., 1993). The diversity and sizes of the Bezymyannyi Formation microfossils decrease toward both the deeper and shallower zones of the basin. It is remarkable that these features are repeated in each of the three large-scale shallowing-upward cycles. The maxima of diversity and abundance of organic-walled microfossils do not exhibit direct correlations with the supposed deposition rates of clayey sediments. These maxima can hardly be explained by dispersion/concentration ratios, since they are not synchronized to the bottom topography changes. To all appearances, they reflect some original distribution of organisms in the basin, i.e., are related to the shelf paleoecological zones. For the time being, it is difficult to identify the most significant reasons for the appearance of such zones, however, it is evident that they are related more to the basin depths than to the distance from the supposed shoreline.

Finally, note that the Riphean deposits of the Turukhansk area compose a rather narrow belt where sequences of an uncertain scale have been tectonically joined, considerably limiting the possibility of paleogeographic reconstructions. Sections of the Pogoryui Formation in the Yenisei Ridge may be good subjects to use in verification of the proposed reconstructions. The sections form extensive fields of outcrops within the region and, to all appearances, correlate with the Bezymyannyi Formation sections. According to the literary data (Semikhatov, 1962; Postel'nikov, 1980), the Pogoryui Formation is most similar to the Bezymyannyi Formation in its peripheral southeastern sections, apparently the nearest to the ancien shoreline. In its western sections, more remote from the sediment sources, the more distal deposits are exposed.

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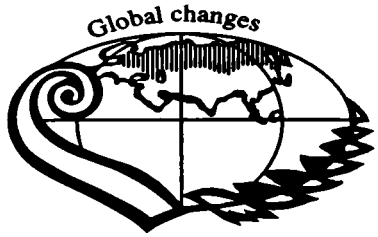

Evolution of the biosphere

Dynamics of Benthic Fauna Diversities at the Cambrian–Ordovician Boundary on the East European Platform and Its Fringing

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Abstract – The second half of the Tremadocian and the beginning of the Arenigian in the Baltic paleobasin are characterized by a distinct tendency of replacement of the uniform benthic fauna, in which few species of the olenidlike trilobites (Swedish-Latvian confacies) or lingulates (North Estonian confacies) dominated, with a new and significantly more diverse fauna, including trilobites and lingulates as well as articulate brachiopods, bryozoans, echinoderms, and ostracods. The biotic crisis corresponding to the first half of the Tremadocian preceded the appearance of this fauna. The crisis resulted in an almost complete extinction of benthic marine biota. The extinction event corresponds to a time of extremely unstable sea level and correlates with a maximum of black shale sedimentation. The appearance of taxa owing to evolution of local lineages becomes comparable with that because of immigration only since the second part of the Arenigian.

The largest evolutionary radiation, which may be regarded rightfully as one of the most important events in the Phanerozoic history of marine biota, corresponds to the Ordovician. During a relatively short period of geological history, covering a few dozen million years, the poorly differentiated Cambrian benthic communities, in which trilobites and lingulates (inarticulate brachiopods with phosphatic-calcitic shell) dominated among skeletal animals, was replaced by a new fauna. Sessile filter feeders such as articulate brachiopods, bryozoans, various echinoderms, and, since the second half of the Ordovician, tabulate and rugose corals occupied a leading role. The diversity of bivalve and cephalopod molluscs and ostracods increased abruptly during the Ordovician; and nematophoran graptolites and first vertebrates appeared (Shergold, 1988).

The first phase of Ordovician radiation, with the final formation of the main benthic communities, typical for a large part of the Paleozoic, corresponds to the Early Ordovician.

The purpose of this study is an analysis of changes in the taxonomic composition, diversity, and structure of benthic communities of epicontinental seas in the initial phase of Ordovician evolutionary radiation, taking the Balto-Scandian paleobasin as an example. R. Mjannil and V. Jaanusson (Jaanusson, 1976) distinguished several biofacies belts in this region, which they called confacies. Fauna from the Swedish-Latvian and the North Estonian confacies is the most interesting from the viewpoint of analysis. This is explained by relatively good, though far from complete in some cases, knowledge of the three main groups: trilobites, lingulates, and articulate brachiopods, in the interval of the Batyrbayan Stage of the Late Cambrian through the Early Ordovician. The analysis of the diversity dynamics is based on taxa of genus level. The data on distribution of 72 polymerous trilobite genera, 15 articulate brachiopod genera, and 12 lingulate genera in the Swedish-Latvian and partly in the Sconenian confacies throughout the Late Cambrian–Early Ordovician are based mainly on publications. Moreover, the data on composition of trilobite complexes in the interval from the *Peltura scarabeoides* Zone to the *Megistaspis estonica* Zone (Fig. 1) may be regarded as full and reliable (Martinson, 1974; Tjernvik, 1956), although the second part of the Arenigian may be considered incomplete. Lingulates with an age younger than the Tremadocian are known (in part) only from the collections of L. Holmer. Articulate brachiopods are rare in the Cambrian through the middle Arenigian being represented by a single genera. Their representative assemblage is known, owing to A. Öpik's studies (Öpik, 1939), only from the late Arenigian *Asaphus expansus* Zone.

The data on distribution of 32 trilobite genera, 37 articulate brachiopod genera, and 31 lingulate genera for the analogous time interval in the North Estonian confacies are based mainly on a restudy of the All-Russian Institute of Geology (St. Petersburg) and Estonian Institute of Geology (Tallinn) collections. This information was only recently and partially published.

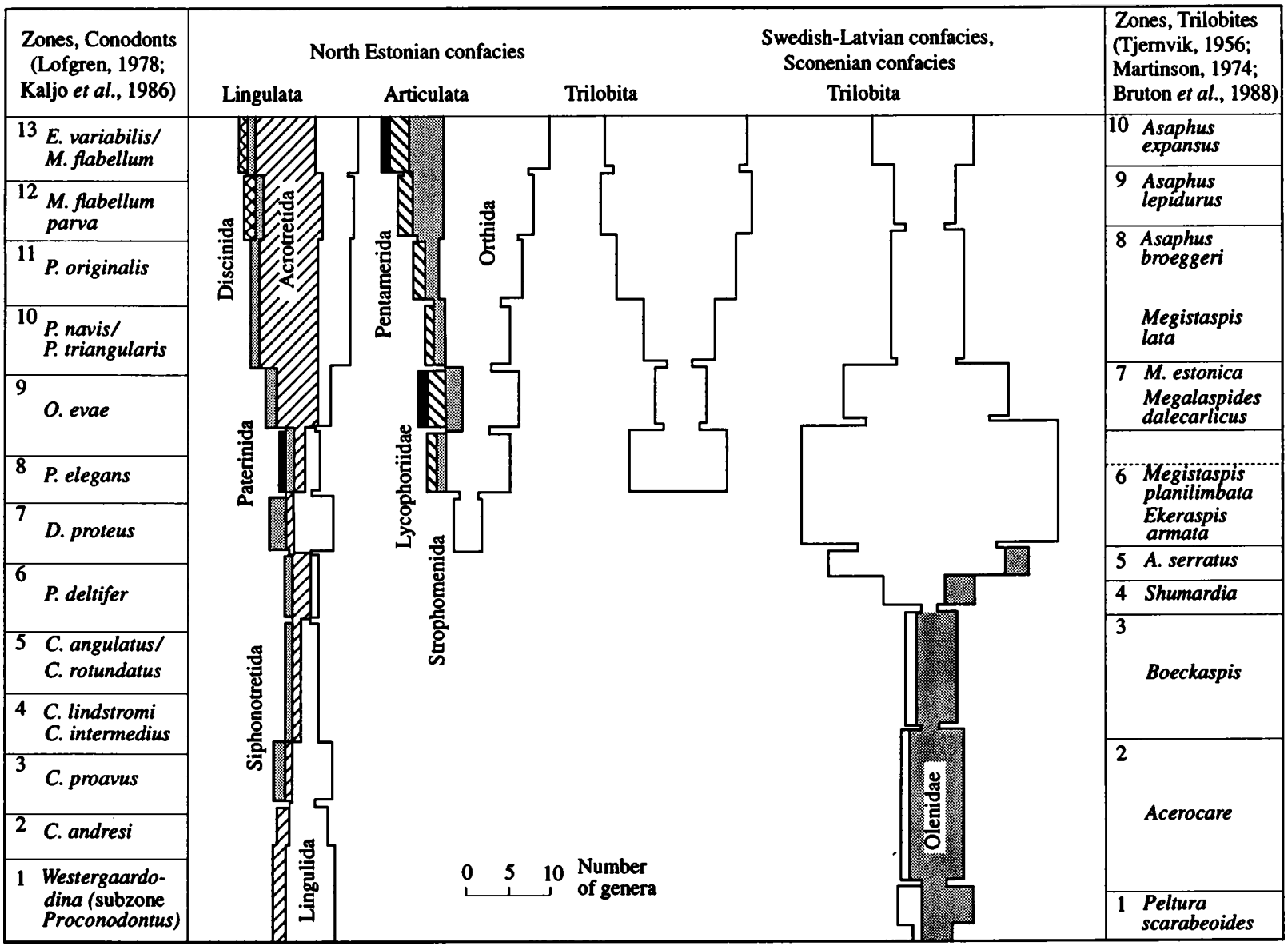

Fig. 1. *Changes in the genera diversity of lingulates, articulate brachiopods, and polymerous trilobites in the Swedish-Latvian, Sconenian, and North Estonian confacies of the Balto-Scandian paleobasin from the Batyrbayan Stage of the Upper Cambrian to the end of the Arenigianian Stage of the Lower Ordovician. The number of transitional, extinct, and appeared genera correlated with the boundaries of zonal subdivisions of conodont zones for the North Estonian confacies and trilobite zones for the Swedish-Latvian and Sconenian confacies is shown.*

This is especially true for the articulate brachiopods and trilobites of the first half of the Arenigian (the Latorpian Horizon).

The available data on the distribution of trilobite, articulate brachiopod, and lingulate genera populating the East European craton periphery and the shelves of microcontinents and ocean islands between the craton and Gondwana in the Late Cambrian–Early Ordovician were also analyzed. The fauna described for the Subpolar and the South Urals, the Czech Republic, southern Germany, and the Swietokrzyskie Mountains in Poland is the most interesting. These data represent a certain interest for paleozoogeographic reconstructions and for defining directions of individual taxa and communities migration. However, they cannot be used for the determination of possible centers of origin of specified communities, which were distributed in the Balto-Scandian paleobasin as a result of immigration, because the Late Cambrian fauna of the above-mentioned regions, except the Swietokrzyskie Mountains, is not known yet.

Two diagrams (Figs. 1 and 2) show the general character of changes in the benthic fauna diversity of the Balto-Scandian paleobasin in the second half of the Late Cambrian through the Early Ordovician. The first diagram illustrates variations in the number of polymerous trilobite, articulate brachiopod, and lingulate genera as well as the ratio between extinct and appearing taxa at the levels corresponding to the main biozonal subdivisions. The second diagram shows the curves of variations in diversity of benthic fauna from the Swedish-Latvian and the North Estonian confacies, compiled using the method of V.Yu. Dmitriev (Dmitriev, 1989).

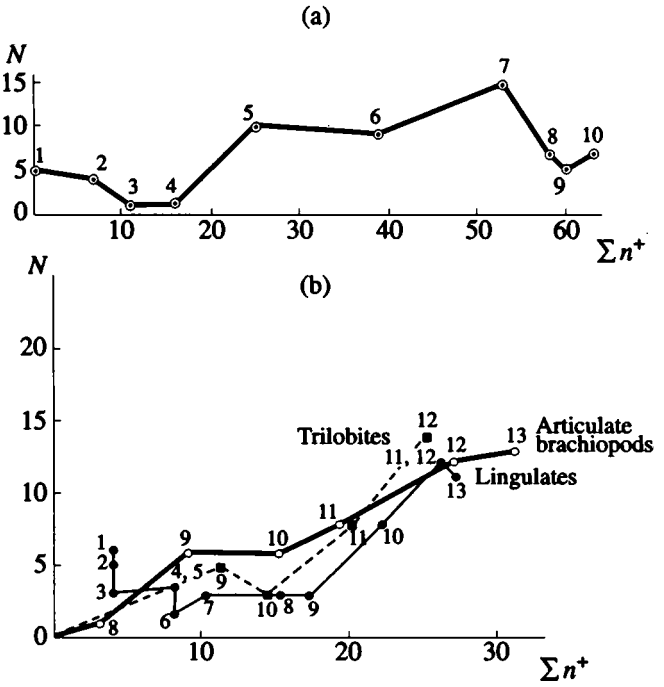

Fig. 2. *Curve of changes in trilobite diversity in the Swedish-Latvian and the Sconenian confacies in the interval from the Peltura scarabeoides Zone to the Asaphus expansus Zone (a), and curves of changes in diversity of lingulates, articulate brachiopods, and trilobites in the interval from the Westergaardolina Zone to the E. variabilis/M. flabellum Zone in the North Estonian confacies (b).*

Horizontal axis shows the number of genera that appeared since the Batyrbayan Stage, vertical axis, the number of transitional genera at the boundaries of conodont and trilobite zones in the North Estonian confacies and the Swedish-Latvian and the Sconenian confacies, respectively.

The general tendency of replacement of relatively uniform benthic fauna during the second half of the Tremadocian to the beginning of the Arenigian is clearly traced in the entire Baltic paleobasin regardless of the significant lithofacies differences between the North Estonian confacies and the Swedish-Latvian confacies. This replacement was characterized by a situation where a few dominant species of olenids (Swedish-Latvian confacies) or lingulates (North Estonian confacies) were replaced by a new, significantly more diverse fauna, including trilobites and lingulates, articulate brachiopods, bryozoans, echinoderms, and ostracods. The differences between the confacies, as well as significant differences in the taxonomic diversity and composition of dominating groups of benthos in the entire Baltic paleobasin, were especially distinct in the Late Cambrian. Significant changes in the lingulate and trilobite complexes took place at the order and the family levels as well. The appearance of this new fauna occurred after the extinction of the majority of trilobite and lingulate genera, many of them representing the last links of evolutionary lineages traced from the beginning of the Late Cambrian and, in some cases, since the Middle Cambrian.

Predominantly silty and sandy carbonate-free sediments were accumulated in the North Estonian confacies from the Late Cambrian through the middle Tremadocian. The wide distribution of unstable sandy substrates predetermined the appearance of specific endemic benthic communities, in which a few species of epibenthic obolids dominated absolutely. The triple biofacies zonality in their distribution with depth is clearly traced (Popov *et al.*, 1989). The simplification of this biofacies zonality due to the extinction of some communities occurred in the *C. proavus* phase through the *C. angulatus–C. rotundatus* phase. The most shallow marine communities with *Ungula* and *Schmidtites*, which were replaced at the beginning of the *C. intermedius* phase by the cryptogenic fauna of lingulates of the *Obolus, Lingulella,* and *Helmersenia* genera (closely related to the *Skolithos* facies), survived. The distribution of the last facies corresponds to the transgressive part of the large sedimentary rhythm initiated after the eustatic minimum at the beginning of the *C. proavus* phase (known also as the Lange Ranch event).

The total extinction of biota in the *C. angulatus–C. rotundatus* phase correlates with a maximum distribution of anoxic environments during the transgressive phase of the next sedimentary rhythm, which occurred after a eustatic minimum, corresponding to the second half of the *C. lindstromi* phase, which is known also as

the Black Mountain event. Primary biological productivity reached a maximum during this time.

Black shale sedimentation with formation of alum shales of the Olenidae Group and of dicktyonem shales, which are related to upwelling along the northwestern margin of the continent, prevailed in the Swedish-Latvian and the Sconenian confacies during the entire Late Cambrian and a greater part of the Tremadocian. Relatively uniform benthic fauna, in which polymerous trilobites of the Olenidae family dominated, populated these environments in the second half of the Cambrian. According to the paleozoogeographic reconstruction proposed by J.H. Shergold (Shergold, 1988) for the Late Cambrian, this fauna belonged to the rather extended Baltic province, which is one of the five provinces determined to exist at this time. The gradual decrease of trilobite diversity occurred during the *Peltura scarabeoides*, *Acerocare*, and *Boeckaspis* phases. Moreover, the majority of genera disappeared at the end of the *Acerocare* phase, and only *Parabolina* was transitional. The complex of olenids at the level of the *Boeckaspis* Zone was renovated almost completely; however, it is not clear whether its appearance was a result of immigration of new fauna, or of transformation of more ancient local taxa. The appearance of typical representatives of *Hysterolenus–Broeggeria* fauna, rather widespread from the *C. proavus* to the *P. deltifer* phase, indicates a possible immigration during the formation of this complex. The appearance of this fauna apparently occurred later with respect to its first appearance in the sections of the Cambrian–Ordovician boundary in Wales (Rushton, 1982) and, perhaps, in the Kendyktas Range of southern Kazakhstan.

The significant renovation of the olenid trilobites in the Baltic paleobasin corresponds to the maximum transgression occurring after the Lange Ranch eustatic event and coincides approximately with the appearance of the first nematophoran graptolites (Kaljo *et al.*, 1986).

The extinction of this fauna corresponds closely to the extinction of obolids at the level of the *C. angulatus–C. rotundatus* phase in the North Estonian confacies. Only three trilobite genera, *Saltaspis*, *Niobella*, and *Peltocare* and species of lingulates, which are typical for the broeggerian community, are transitional.

The following sharp increase of benthos diversity in the Balto-Scandian basin was a result of four successive immigration waves, between the end of the Tremadocian and the first half of the Arenigian. Two of these correspond to the beginning of the *D. proteus* and the *P. elegans* phase and coincide with the transgressive parts of the sedimentary rhythms of the second order in the larger sedimentary rhythms of the major early Arenigian transgression (Fortey, 1984).

The first wave of immigration, corresponding to the *Shumardia* and *A. serratus* phases, is recorded only in the Swedish-Latvian and the Sconenian confacies. It is associated with a distribution of so-called ceratopygean fauna. The species of *Shumardia*, *Ceratopyge*, *Apatokephalus*, *Dikelokephalina*, *Symphysurus*, *Platypeltoides*, *Harpides*, *Varvia*, *Euloma*, *Parapilekia*, *Orometopus* and other genera are diagnostic for this fauna. A more than four-fold increase in taxonomic diversity (Fig. 1; Fig. 2b, dots 4 and 5) occurred mainly because of immigrants related to more ancient fauna of D. Shergold's South China Province (Shergold, 1988). It is possible that ceratopygean fauna appeared on the southeastern periphery of the East European craton somewhat earlier in the first half of the Tremadocian. In any case, the presence of short-lived *Jujiyaspis* (= *Alimbetaspis*) genus recorded in the ceratopygean trilobite complex of the South Urals (Balashova, 1961) gives some basis for this affirmation.

Changes in the benthos composition in the Swedish-Latvian confacies at the end of the Tremadocian proceeded in the background of the gradual cessation of black shale sedimentation changing into carbonate accumulation. The late Tremadocian seems to be a time of stasis for benthic fauna of the North Estonian confacies. Only four genera of lingulates, including two transitional genera, are known here from deposits of this age. The first glauconitites since the second half of the Tremadocian appear and black shale sedimentation ceases, which apparently reflects a significant decrease in the biological productivity of the basin.

The following wave of migration occurred at the beginning of the Arenigian, corresponding to the *D. proteus* phase. It resulted in a further increase in trilobite diversity in the Swedish-Latvian confacies mainly because of the appearance of numerous genera of asaphids such as *Megistaspis*, *Ekeraspis*, *Megalaspides*, *Lapidaria*, *Lannacus*, and *Hunnebergia*. Extinction at this level resulted in the disappearance of trilobites and lingulates typical of the broeggerian community (Fig. 1).

The diverse lingulate community is characteristic of the North Estonian confacies during the *D. proteus* phase (Löfgren, 1978). The representatives of the *Thysanotos*, *Leptembolon*, *Acrotreta* genera and siphonotretids are most typical for this community. This fauna definitely existed in the area of the Czech Republic since the beginning of the Arenigian (Havliček, 1982). It is also known from the Swietokrzyskie Mountains, in southern Germany, and the South Urals. Apparently, the community with *Thysanotos* and *Leptembolon* appeared in one of the marginal basins on the southern or southwestern periphery of the East European craton, and its distribution had a circumcratonic character.

The clearly displayed diversification at the level of the *P. elegans* phase in the North Estonian confacies represents a final level, where the increase in diversity was caused mainly by an immigration of the new benthic fauna. The synchronous appearance of main groups of benthic fauna, which were typical for the Balto-Scandian basin through the Ordovician and are unknown in the more ancient benthic communities (Figs. 1 and 2a), occurred at this level with the beginning of carbonate sedimentation. The majority of appearing taxa are of cryptogenic origin. For example, bryozoans, brachiopods of the *Strophomenida* order,

and encrinurid trilobites are now here recorded in the more ancient deposits. The only exception are, probably, trilobites because the majority of the genera and species appearing at this level are definitely related to synchronous or somewhat more ancient complexes of the Swedish-Latvian confacies. Note that the trilobite diversity at the level of the *P. elegans* and the *O. evae* conodont zones decreases significantly in this confacy.

Furthermore, the slow increase in the total benthos diversity occurred during the Arenigian in the North Estonian confacies. The appearance of new taxa because of both the divergence and transformation in the lineages of local origin became comparable, or even prevailed in terms of quantity, over their immigration.

Thus, the significant increase in total diversity of benthic fauna at the end of the Tremadocian through the beginning of the Arenigian in the Balto-Scandian basin is a result of several successive immigrations. Even though the taxa, which appeared including mainly bryozoans, articulate brachiopods, and trilobites, had formed already mature communities, their origin remains, in many cases, unclear. A definite connection with the more ancient fauna of the South China province (Shergold, 1988) was established only for ceratopygean fauna of trilobites distributed in Balto-Scandia in the late Tremadocian.

Since the second half of the Arenigian, the appearance of new taxa because of the evolution of local lineages becomes comparable with the immigration input.

The biotic crisis, corresponding to the first half of the Tremadocian, occurred before this event. This crisis resulted in almost complete extinction of the benthic constituent of marine biota. The extinction event corresponds to a time of extremely unstable sea level and maximum distribution of black shale sedimentation in the Balto-Scandian basin.

The short-lived communities with a wide geographic distribution exceeding the limits of the marginal seas that existed on the periphery of the East European craton, appear in the Balto-Scandian basin during the time interval, which preceded levels of maximum immigration of new fauna. Fauna with *Broeggeria* and *Hysterolenus* from the Swedish-Latvian confacies, and the lingulate assemblage with *Thysanotos* and *Leptembolon* from the North Estonian confacies may serve as an example of these types of communities.

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Evolution of the biosphere

Early Tremadocian Acritarch Taxonomic Composition and Climate of the Baltic Phytoplankton Province

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Abstract – The taxonomic composition of the early Tremadocian acritarchs in the temperate Baltic phytoplankton province was similar to that of the cool Mediterranean province. The early Tremadocian climate in temperate latitudes is presumed to have been a cold one. Conceivably it was the result of two large regressive eustatic events that occurred at that time and are thought to be of glacial origin.

Provincialism of the Ordovician phytoplankton was established as early as the 1970s (Rauscher, 1973; Vavrdova, 1974). The former author distinguished two provinces in the European Ordovician, namely, the North African to South-Middle European and the Northern, to which he referred the Baltic–Russian platform. M. Vavrdova also established two provinces, the temperate Baltic, with the predominance of acanthomorphids, and the Mediterranean, with prevailing diacromorphids. She included northern Russia, Sweden, Poland, northern Germany, and, supposedly, part of the British Islands into the Baltic province, whereas the Mediterranean province embraced Belgium, France, Spain, northern Africa, southern Germany, central Bohemia, and Bulgaria. She remarked that though the plankton geographical differentiation was vague in the Tremadocian, it became more clear beginning with the Arenigian.

More recently, German scholar R. Wolf (Wolf, 1980; Welsch, 1986), studying Tremadocian acritarchs of Spain, more thoroughly characterized the Baltic and Mediterranean provinces established by Vavrdova. In his opinion, *Baltisphaeridium* dominated in the Tremadocian of the Baltic province, and *Saharidia* was absent in this region, whereas *Vulcanisphaera* distribution was limited to the southern Poland. In the Mediterranean province, the Tremadocian was characterized by the predominance of Diacromorphitae and Herkomorphitae subgroups and by the presence of *Saharidia*, *Vulcanisphaera*, *Goniosphaeridium*, and *Micrhystridium*.

In 1986, another German scholar, M. Welsch (1986) studied acritarchs from the Digermul Group, northern Norway, whose age, according to trilobites and graptolites, ranged from the middle Cambrian to the early Tremadocian. In the chapter devoted to provincialism and facies dependence of phytoplankton, Welsch gave a review of preceding papers, which dealt with the Ordovician acritarch provinces, and concluded that northern Norway belonged to the Mediterranean province. This suggestion was based on the predominance of Diacromorphitae and Herkomorphitae in the early Tremadocian phytoplankton (microfloras *AVa, b* and *AVI*) and on the presence of genera *Multiplicisphaeridium*, *Goniosphaeridium*, and *Vulcanisphaera* among Acanthomorphitae. Moreover, *Baltisphaeridium* was represented by rare specimens of a single species. However, according to the Cambrian–Ordovician boundary palinspastic map of the southern hemisphere (Erdtmann, 1982), northern Norway was located in temperate latitudes. In order to explain the presence of cold-water phytoplankton in the region, Welsch suggested the occurrence of a cold current, which moved along the western shelf of the Baltic–Russian platform and penetrated far northward, as shown in the Fig. 1. He also noted the influence of the temperate Baltic province in the region that especially distinctly resulted in the *AVa* microflora composition, which yielded such typical Baltic forms as *Ooidium rossicum* Tim and *Multiplicisphaeridium cervinacornua* Welsch. In his opinion, the occurrence of these species in the *AVa* microflora permits the attribution of it to the Tremadocian. The species were found in the Obolus Beds of the Baltic region, which Welsch assigned to the Tremadocian, using the old data of B.V. Timofeev (1959; 1966). According to modern view, the lower part of the Obolus Beds (the Yulgase Formation, the base of the Maardu member of the Kallavere Formation in Estonia, and the Ladoga Formation of Leningrad region), based on conodonts (Borovko and Sergeeva, 1985), is referred to the Upper Cambrian. *O. rossicum* and *M. cervinacornua* (= *Vogtlandia* sp. after Borovko *et al.*, 1984; Volkova, 1989a) are known only from the lower part of the

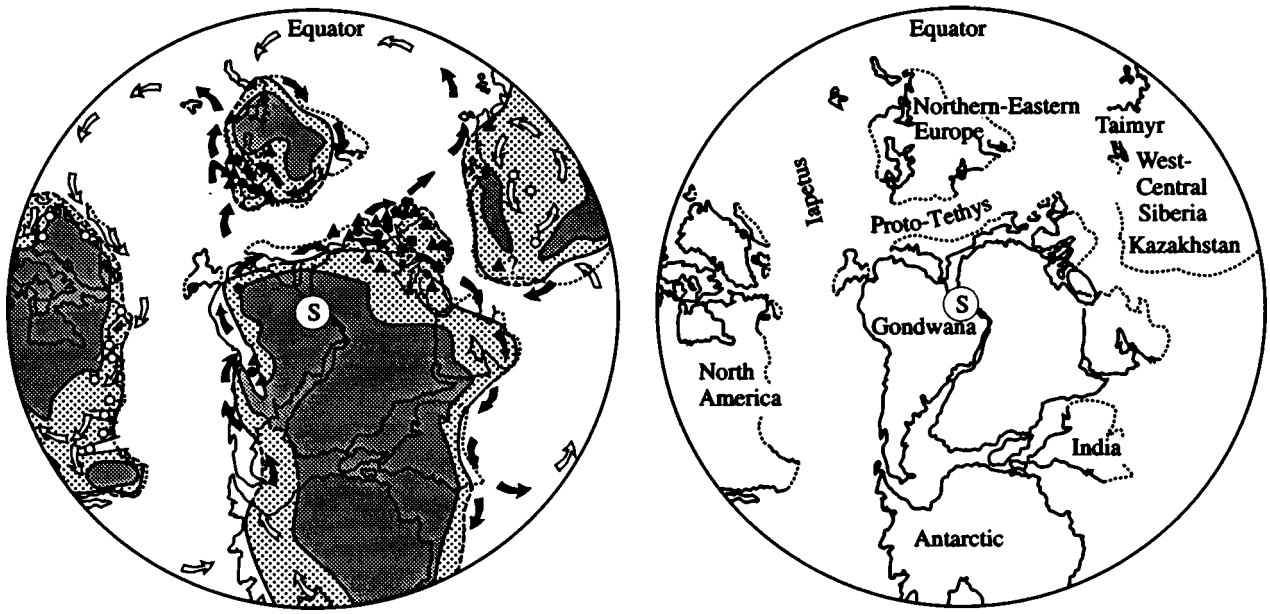

Fig. 1. *Early Ordovician palinspastic map of the southern hemisphere (Erdtmann, 1982, changed). Arrows indicate currents: light – supposedly warm-water, with points – supposedly temperate, black – supposedly cold-water.*

Obolus Beds, from both the Ladoga Formation, and the base of the Maardu member (*Proconodontus* and *Cordylodus andresi* zones). They were not recorded in the early Tremadocian (*Cordylodus proavus* Zone). Taking into account this data, *AVa* microflora, which was influenced, according to Welsch, by the temperate Baltic province, must be referred to the Late Cambrian. Abundant *Acanthodiacrodium* cf. *A. spinum* Rasul, found there, a species very similar, if not identical, to *Acanthodiacrodium timofeevii*. Golub et Volk., also confirms this conclusion. The latter species is widespread in the Ladoga Formation sediments. Well-preserved graptolites and trilobites were not recorded in the part of the section with *AVa* microflora. Only a trilobite *Parabolina* sp. was found there. *AVa* microflora yields taxa common with the acritarch assemblage from the Late Cambrian *Peltura* Zone of the Baltic region and Moscow syneclise (BK4B assemblage in Volkova, 1990).

As stated above, Welsch explained the Mediterranean character of the early Tremadocian *AVb* and *AVI* microfloras of the Digermul Group, with a predominance of Diacromorphitae and Herkomorphitae (*Rhabdinopora flabelliforme* and *Clonograptus tenellus* zones), by the occurrence of a cold current. Nevertheless, the phytoplankton, very similar to that of the Mediterranean, also occurred in the early Tremadocian of the Baltic region, which referred to the temperate Baltic province. At that time, the Baltic region was influenced by a warmer current (Fig. 1) from the equatorial latitudes (Erdtmann, 1982).

Recently, I studied early Tremadocian acritarchs from the *Rhabdinopora flabelliforme* graptolite zone and *Cordylodus proavus-C. rotundatus-C. angulatus* conodont zones in Estonia and in the Leningrad region (Volkova, 1989a, 1989b). In some sections of the Estonian glint line, namely, in the Vihula and Suhkrumyagi exposures and the Maardu-9 borehole, Diacromorphitae and Herkomorphitae predominated in the phytoplankton of the *C. proavus* Zone (Volkova, 1989a). Diacrodians, represented by *Acanthodiacrodium*, *Arbusculidium*, *Dasydiacrodium*, *Priscotheca*, and *Trachydiacrodium*, constitute from 15 to 35% of the assemblage (Table 1). Phytoplankton of this zone was named as the assemblage with *Acanthodiacrodium angustum*, *Dasydiacrodium ornatum*, and *Arbusculidium striatulum* (Volkova, 1989b). Taxa referred to Herkomorphitae (genera *Cristallinium*, *Cymatiogalea*, *Cymatiosphaera*, and *Stelliferidium*) are more numerous, their amount ranging from 32 to 54%. The genus *Baltisphaeridium*, represented by two species, is an insignificant component, ranging from 0.5 to 7.0%. A few species of the genus *Vulcanisphaera* are present as well. Study of acritarchs from younger, early Tremadocian conodont zones, namely, *C. lindstroemi* and *C. rotundatus–C. angulatus*, in the Estonian glint sections and in the Leningrad region (exposures near Toila and the Syas' River) also revealed abundant diacrodians and herkomorphids in the phytoplankton assemblage of that time (Volkova, 1989b). For example, in the acritarch assemblage from the Vihula and Orasoya members of the Lakhemaa Formation near Toila, the diacrodians constitute from 14.0 to 52% (Table 1), and herkomorphids range from 7.5 to 34%, whereas *Baltisphaeridium* does not exceed 4.0%. The presence of *Vulcanisphaera* is noteworthy, represented by *V. britannica* Rasul and *V. imparila* Rasul, which were described from the Tremadocian of England (Rasul, 1976). In some samples, this genus reaches 19.5%. The dictyonem shales (Toolse and Tyurisalu members in the

Table 1. Number (%, except stated specimens) of major acritarch morphologic types in lower Tremadocian sections of the glint line of Estonia and the Leningrad region (Volkova, 1989a, b) and in lower Tremadocian of the Digermul Group, northern Norway (Welsch, 1986)

Taxa	Glint line of Estonia and Leningrad region											Northern Norway	
	Zone *Cordylodus proavus*					Zones. *C. lindstroemi–C. angulatus–C. rotundatus*						Zones *R. flabelliforme–C. tenellus*	
	Vihula section		Suhkrumyagi section		Maardu-9 borehole	Section near Toila						Sections in the Digermu Peninsula	
	samples											microflora	
	17/7	49/4	S843A	S842A	131.4 m	E45/8	E45/9	E45/10	E45/11	E45/12	E45/13	*AVb*	*AVI*
Diacromorphitae	27.5	35.0	15.0	27.5	16.0	51.0	52.0	16.5	14.0	25.0	33.0	15.60	8.51
Herkomorphitae	42.0	32.0	32.5	54.0	51.5	13.0	7.5	18.0	34.0	31.5	25.0	32.3	63.83
Baltisphaeridium	7.0	7.0	0.5	0.5	4.0	3.5	2.0	0.5	0.5	4.0	1.0	1 - 5 specimens	1 - 5 specimens
Vulcanisphaera	0.5	0.5				19.5	9.5	1.0	0.5				

exposure near Toila and the top of the Kopor'e Formation on the Syas' River) are the only exception. They are characterized by the predominance of sphaeromorphids (*Leiosphaeridia*, "Eisenack loops"). The peculiar composition of the phytoplankton assemblage in the shales appeared to result from the specific environments of their accumulation in shallow, baylike basins (Lapo and Mikhailova, 1988). Nevertheless, rare diacrodians and *Vulcanisphaera* were recorded in them.

In the early Tremadocian *AVb* and *AVI* microfloras of the Digermul Group, the diacrodians constitute 15.6 and 8.51%, respectively, whereas herkomorphids, 32.3 and 63.83%. *Baltisphaeridium* is represented by rare specimens, whereas *Vulcanisphaera* and *Saharidia* are absent (Welsch, 1986).

Presented data shows that in both regions, northern Norway and the Baltic region, Diacromorphitae and Herkomorphitae were rather important in the early Tremadocian phytoplankton assemblage (Plate 1), and *Baltisphaeridium* had a subordinate position. The phytoplankton assemblage also included *Goniosphaeridium*, *Micrhystridium*, and *Vulcanisphaera*. Only *Saharidia* was not recorded. However, *Saharidia* is known from the Upper Cambrian–lower Tremadocian beds of the Moscow syneclise (Volkova, 1990). Accordingly, the criteria suggested for defining the Baltic province in the early Tremadocian, namely, the predominance of *Baltisphaeridium* and the absence of *Vulcanisphaera* and *Saharidia* (Welsch, 1986), are invalid. In that period, the phytoplankton composition was almost identical, both in high and temperate latitudes.

In Welsch's opinion, paleoclimate was the principal factor of the early Ordovician phytoplankton spatial distribution affecting water temperatures, as was previously established for the Silurian (Cramer and Diez, 1974). We can suggest that the early Tremadocian climate in temperate latitudes was cold and similar to that of high latitudes. Most likely, it was the result of the eustatic Acerocare Regressive Event (ARE) and the Peltocare Regressive Event (PRE), which occurred at that time and are thought to be of a glacial origin (Erdtmann, 1986). Two glaciations, one at the beginning and one at the end of the early Tremadocian, could have resulted in a general cooling in temperate latitudes. Regarding the warm low-latitude province, in the early Tremadocian phytoplankton assemblage recorded in the Jilin Province of northeastern China (Yin, 1986) and in the Alberta Province of Canada (Martin, 1992), the genera and species diversity of diacrodians and herkomorphids became strongly impoverished. In lower latitudes, the phytoplankton at this level is characterized by the presence of forms with peculiar morphology, e.g., the genera *Corollasphaeridium* and *Goniomorpha*, which were hitherto found only in the mentioned regions.

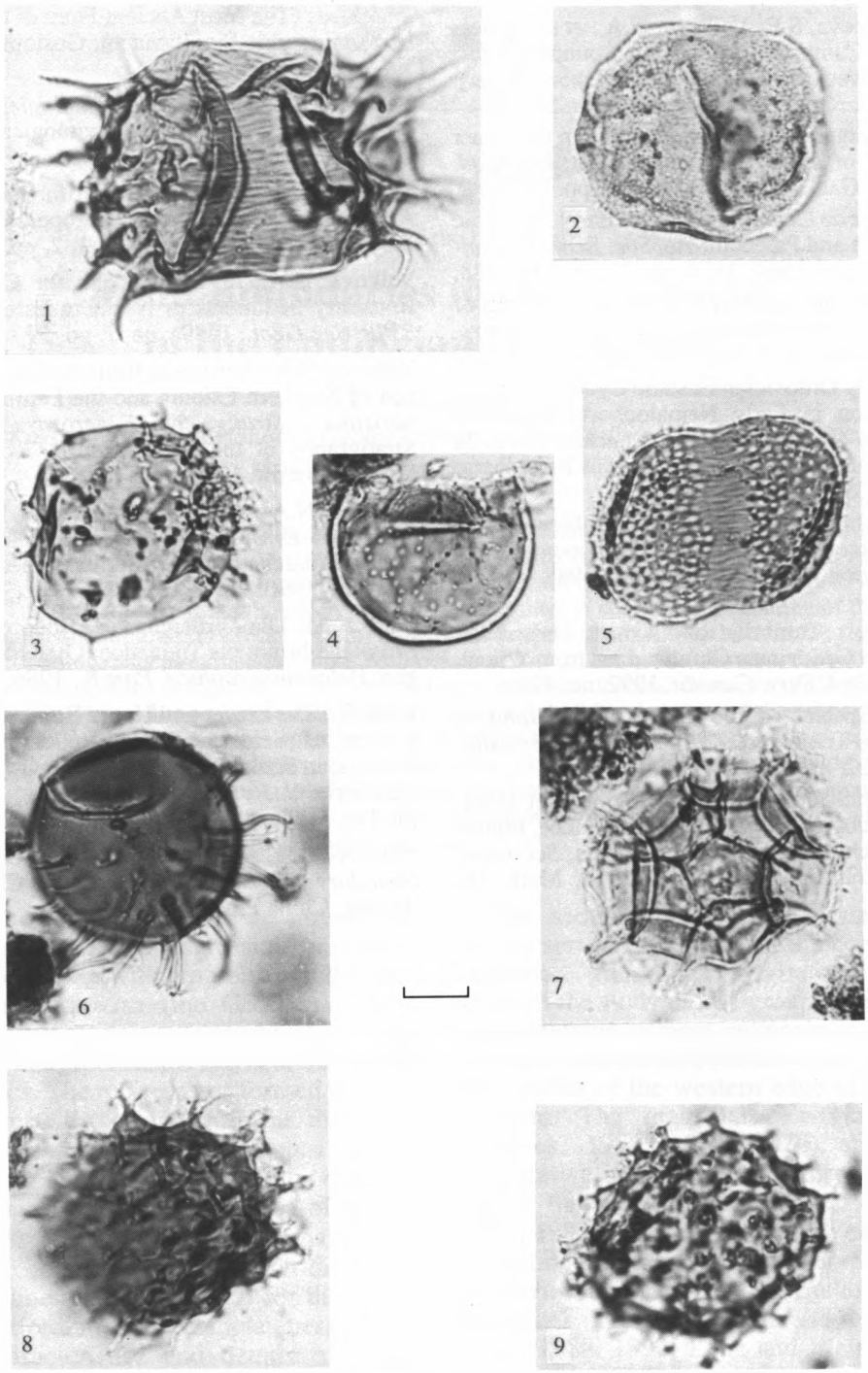

Plate 1. *Early Tremadocian acritarchs of the Baltic province.*

Length of scale bar is 10 microns.

Subgroup Diacromorphidae (1 - 3, 5): 1 – *Acanthodiacrodium ubui* Martin; slide GIN 3937/06377 – 4; section near Toila, sample E 45/9; Lakhemaa Formation, Vihula member; 2 – *A. comptulum* Rasul; slide GIN 3937/06880 – 1; Estonia, Suhkrumyagi section, sample Su-84-1A, Kallavere Formation, Maardu member; 3 – *Arbusculidium rommelaerei* Martin; slide GIN 3937/06378 – 1; Estonia, section near Toila; sample E 45/8A; Lakhemaa Formation, Vihula member; 5 – *Acanthodiacrodium angustum* (Downie) Combaz; slide GIN 3937/06378 – 2; Estonia, section near Toila, sample E 45/8; Lakhemaa Formation, Vihula member.

Subgroup Herkomorphitae (4, 6, 7): 4 – *Cymatiogalea cuvillieri* (Deunff) Deunff; slide GIN 3937/06393 – 1; Estonia, section on the Suuriygi River below Vihula; sample E 49/4; Kallavere Formation, Maardu member; 6 – *Stelliferidium cortinulum* (Deunff) Deunff *et al.* slide GIN 3937/06378 – 2; Estonia, section near Toila, sample E 45/8; Lakhemaa Formation, Vihula member; 7 – *Cymatiosphaera* sp.; slide GIN 3937/06378 – 2; same locality.

Subgroup Acanthomorphitae (8, 9): 8 – *Vulcanisphaera britannica* f. 1 Rasul; slide GIN 3937/06378 – 1; Estonia, section near Toila, sample E 45/8; Lakhemaa Formation, Vihula member; 9 – *Vulcanisphaera imparila* f. 4 Rasul; slide GIN 3937/06378 – 2; same locality.

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Evolution of the biosphere

Main Boundaries in the Evolution of the Ludlovian Graptolites

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Abstract – The new Ludlovian graptolite fauna appeared and became abundant at the end of the Homerian after a mass extinction event. Its origin is connected with a conservative pristiograptid stem represented by a single-species ancestor, serving as a base for the more complex morphotypes progressively developed in the Late Silurian. The maximum taxonomic differentiation of graptolites is seen at the beginning of the Ludfordian as a result of subsequent radiation events. However, even in the period of the short stasis, they are essentially less diverse morphologically as compared to the Wenlockian forms. In the late Ludlovian, the extinction events often disturb the stasis of the pelagic communities and define the direction and character of the following morphological changes. These changes take place under the stiff model of development of the monograptid colony and are expressed mostly on the thecal apertures, which reveal their adaptive nature. A high speciation rate, background extinction, and frequent replacement of morphoecological types in consistently developing communities are typical for the Ludlovian graptolites. Inverse correlations of diversity of synchronous plectograptid and monograptid faunas testify, apparently, to a different adaptive response of colonies with a reticulate and complete periderm to the same ecological reorganizations.

Black shale facies, widely spread as a result of a powerful post-Wenlockian transgression, represent mostly pelagic rock masses with graptolites in the sections of the lower Ludlovian (the Gorstian). Their sedimentation took place paleogeographically along the periphery of the marginal basins and near the feet of the continental slopes. The rock masses formed in these environments are usually of insignificant thickness and compose well-characterized continuous faunal sequences, providing conditions for highly detailed biozonal stratigraphy. The wide distribution of bathypelagic terrigenous and carbonate rock masses of turbidite origin, the accumulation of which disturbed the black shale sedimentation, is typical for the upper Ludlovian (the Ludfordian). The completeness of the paleontological characteristics and details of zonal sequences suffers from a declining volume of graptolitic argillites, up to thin interlayers among sandstones and calcarenites in many areas (Canadian Arctic, Arctic Russia, Central Europe, and others). In this respect, the number of the Ludlovian graptolite zones varies from 3 to 11 in different regional schemes. The sequence of enlarged standard zones (Koren', 1984), used with small changes in this work, was determined for wide interregional correlations. This scale allows including into analysis with minimal error the sections with different states of paleontological characteristics and inadequate detail of the local zonal subdivision.

The sections of Great Britain and continental Europe served as a basis for the concepts on the early Ludlovian graptolites, beginning with the earliest stages of the study of this group. The new faunas of the late Ludlovian, almost unknown in the classic Britain sections, were studied for the first time in the marginal basin facies of the western edge of the East European Platform. The main basic works of A. Urbanek (Urbanek, 1958, 1966, 1970) are devoted to the comparative analysis of the morphology and phylogeny of the Ludlovian graptolites. P.D. Tsegel'nyuk (1976, 1981; Silur, Podalii, 1983) carried out the latest interesting study on the Upper Silurian graptolites in Volyn'. The study of the Ludlovian deposits with graptolites in Arctic Canada and the South Tien Shan (Lenz, 1988, 1990; Lenz and Melchin, 1987; Koren' *et al.*, 1986, 1988) widened and specified considerably the conceptions on the assemblage composition and stratigraphic ranges of many diagnostic taxa.

The sequence from the *Nilssoni–Colonus* up to the *Parultimus* graptolite zones corresponds to the Ludlovian Stage of the Standard Stratigraphic Scale according to modern definition of its boundaries (Bassett, 1985). Graptolite fauna, typical of this stratigraphic interval, was represented mostly by monograptids and passed the peak of maximum diversity much earlier, in the second half of the Landoverian (70 - 75 species in the *Gregarius* and *Turriculatus* zones (Koren' and

Rickards, 1979; Loydell, 1991). In the Wenlockian, the taxonomic composition of zonal associations was reduced by up to 20 - 25 species in one zone and remained approximately constant almost up to the complete extinction of the Early Silurian phyletic lines at the end of the *Lundgreni* Zone (Jaeger, 1991; Koren', 1991; Koren', 1992). The acute reduction of the species number and morphological diversity in the limits of all subfamilies of that time (Plectograptinae, Monograptinae, and Cyrtograptinae) is an indicator of this crisis. The species composition of the first two subfamilies was reduced up to one taxon, whereas the cyrtograptids became extinct entirely. Soon after this event, at the beginning of the *Nassadeubeli* Zone, the divergence of the conservative stem of the transit *Pristiograptus dubius* took place, resulting in the appearance of two new lines: *idoneus–sherrardae* and *praedeubeli–ludensis*. The late Homerian time in monograptid evolution corresponds to the post-crisis interval, when morphologically uniform assemblages had wide geographical ranges. The arising ecosystems were more favorable for the adaptation of plectograptids with a lightened reticulate periderm, after which the short interval of *nassa–dubius* entered a diversification phase. The plectograptids reached a maximum in diversity, which was realized in the existence of quite different specialized colonies by the beginning of the *Ludensis* Zone, when the number of monograptids was reduced again by up to 2 or 3 species. The extinction event at the end of the *Ludensis* Zone affected mostly the plectograptids.

The reappearing graptolite fauna spread intensively at the beginning of the Ludlovian transgression. The main changes in the directions of graptolites morphological evolution at the Wenlockian–Ludlovian boundary are the following:

(1) a disappearance of thecal cladiums, with a following domination in assemblages of usual monograptid colonies up to the end of the Silurian;

(2) a reduction in the diversity of the theca morphotypes as a result of the disappearance of colonies with triangular isolated thecas having original apertural structures;

(3) a replacement of the priodonic theca by the uncinate theca with developed dorsal or dorso-lateral hoods and a noticeable decrease in dimension of the colonies;

(4) considerably more noticeable changes of sicula forms and dimensions in several lineages in the background of a general reduction in diversity of the colony forms;

(5) domination of the apertural structures of thecas in the form of paired lateral lobes – the most successful morphoecologic type among all known in the Ludlovian.

Consequent morphological changes concentrate mostly on the theca apertures lending to complicating apertural structures. The tendencies of lengthening and superposition of thecas in different species groups and in genera with a comparatively stable structure of theca apertures are less typical. In some lineages, the development takes place in accordance with direction of the phyletic evolution; in others, this process becomes interrupted by the divergence events. The appearance of the gomeomorphic structures in the theca apertures is also typical for the co-developing lineages. A maximal taxonomic differentiation of the Ludlovian graptolites of up to 20 - 25 simultaneously existing species is reached at the beginning of the Ludfordian (Fig. 1). However, even in the period of short evolutionary equilibrium (the *Leintwardinensis* Zone), they remain considerably less diverse in the morphotypes than the Wenlockian graptolites. Almost all known phyletic lines reach extreme specialization of thecas and become extinct at the end of the Ludlovian, leaving an ecological niche for the new early Pridoli fauna, which developed even in the more limited combination of morphotypes.

The analysis presented below of the dynamics of the Ludlovian graptolite diversity in the consequent zonal intervals is based first on the results of a centimeter by centimeter sampling of the condensed black shale section of the Kursala Formation in the Alai Range (Figs. 2 and 3). The graptolite zones *Nilssoni–Colonus*, *Scanicus–Chimaera*, *Leintwardinensis*, *Cornutus–Podoliensis*, and *Formosus–Spineus* (Koren' and Rinenberg, 1988; Koren', 1992), are distinguished here in the key sections along the Peshkaut Valley and near Tul' Village. The underlying and overlying deposits contain a continuous sequence of the graptolite zones of the upper Wenlockian and lower Pridolian. The diapasons of the distribution of the main members of the assemblage and the boundaries of the distinguished zones are reliably defined in the Kursala Formation (Fig. 1). This allows the analysis of changes of different scale in the morphological and taxonomic diversity, not only across the zone boundaries, but also within the zonal intervals (Figs. 2 and 3). The biostratigraphic data on the sections of the Gorstian and lower Ludfordian deposits in Great Britain (Rickards, 1976), the Melnik and Siedlce Beds of Poland (Urbanek, 1966, 1970), the Tirit-Ulich deposits of Volyn' (Tsegel'nyuk, 1976, 1981), the Kopanina Beds of the Barrandien (Přibyl, 1983; Kříž *et al.*, 1986), and the Cape Phillips Formation of Arctic Canada (Lenz, 1990) are also used in estimating the general trends in diversity of the Ludlovian graptolites.

The diagram of the dynamics diversity of the Ludlovian monograptid species (Fig. 4) shows a definite degree of symmetry with a clear maximum of diversity at the end of the *Leintwardinensis* Zone. The rate of attainment and the following loss of diversity are approximately commensurable. The diversification of the early Ludlovian graptolites is stepwise as a result of the radiation events at the beginning of zones *Nilssoni–Colonus*, *Scanicus–Chimaera*, and *Leintwardinensis*.

The deepest morphological transformations characterize an initial phase of the Ludlovian radiation (Fig. 4, R_2), when the new progressive lineages appear, having a tendency toward gradual complication of the apertural apparatus of the theca. The late Homerian

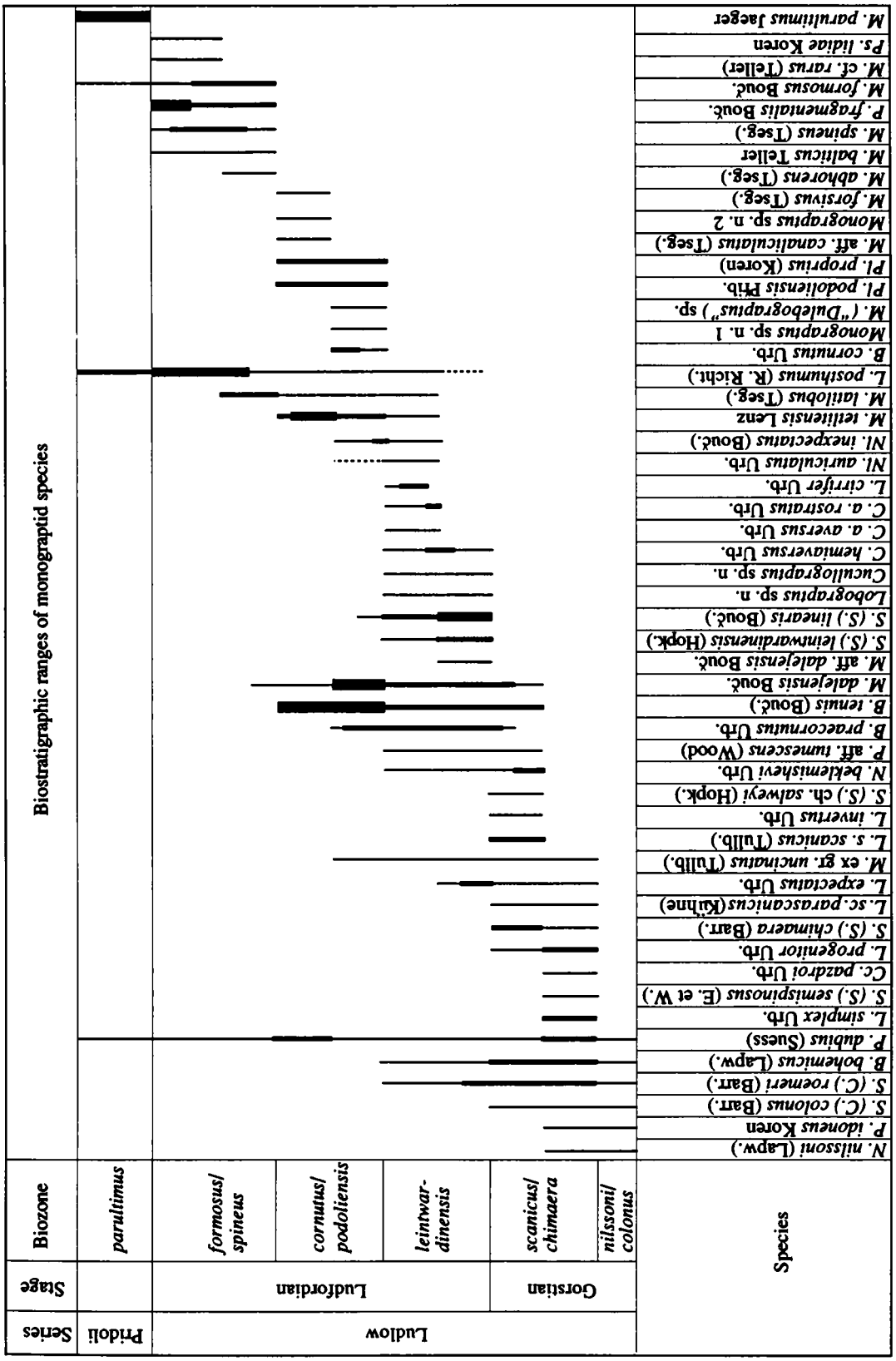

Fig. 1. *Stratigraphic distribution of the Ludlovian monograptids in the Kursala Formation sections of the Alai Range.*

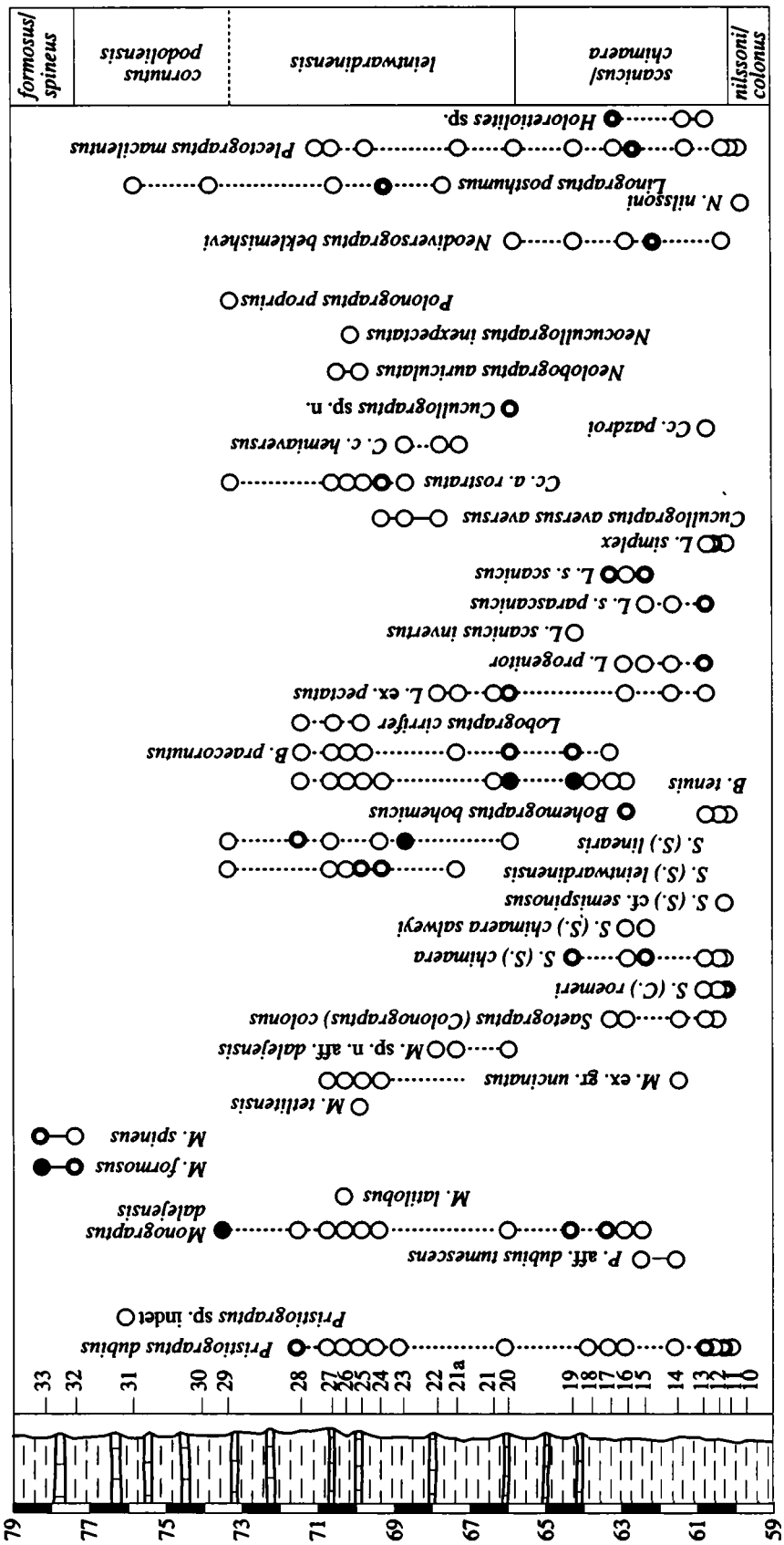

Fig. 2. *Stratigraphic section of the Ludlovian deposits with graptolites, the Kursala Formation, Peshkaut Valley, section 24-A.*

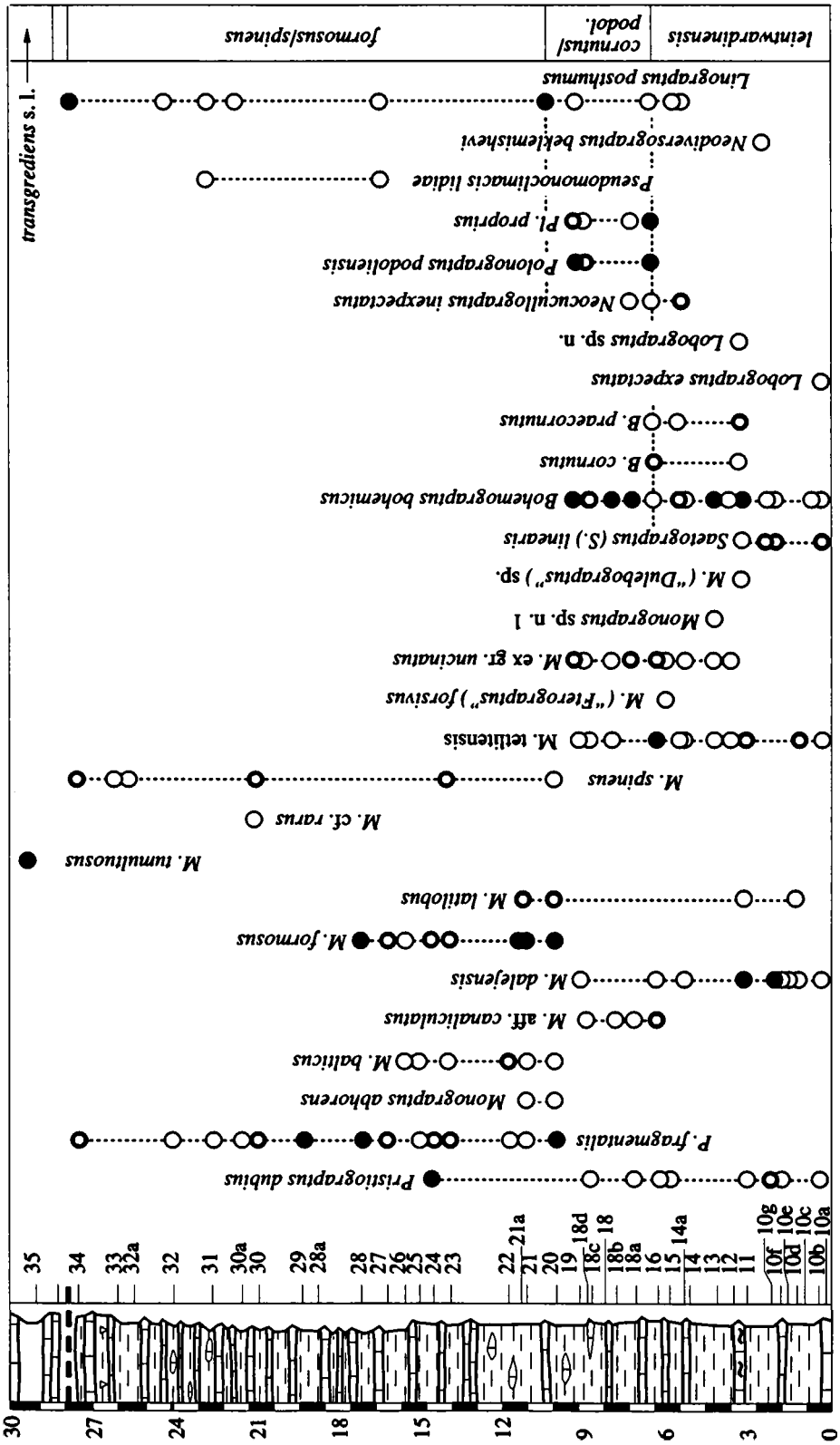

Fig. 3. *Stratigraphic section of the Ludfordian deposits with graptolites, the Kursala Formation, the Peshkaut Valley, section 26.*

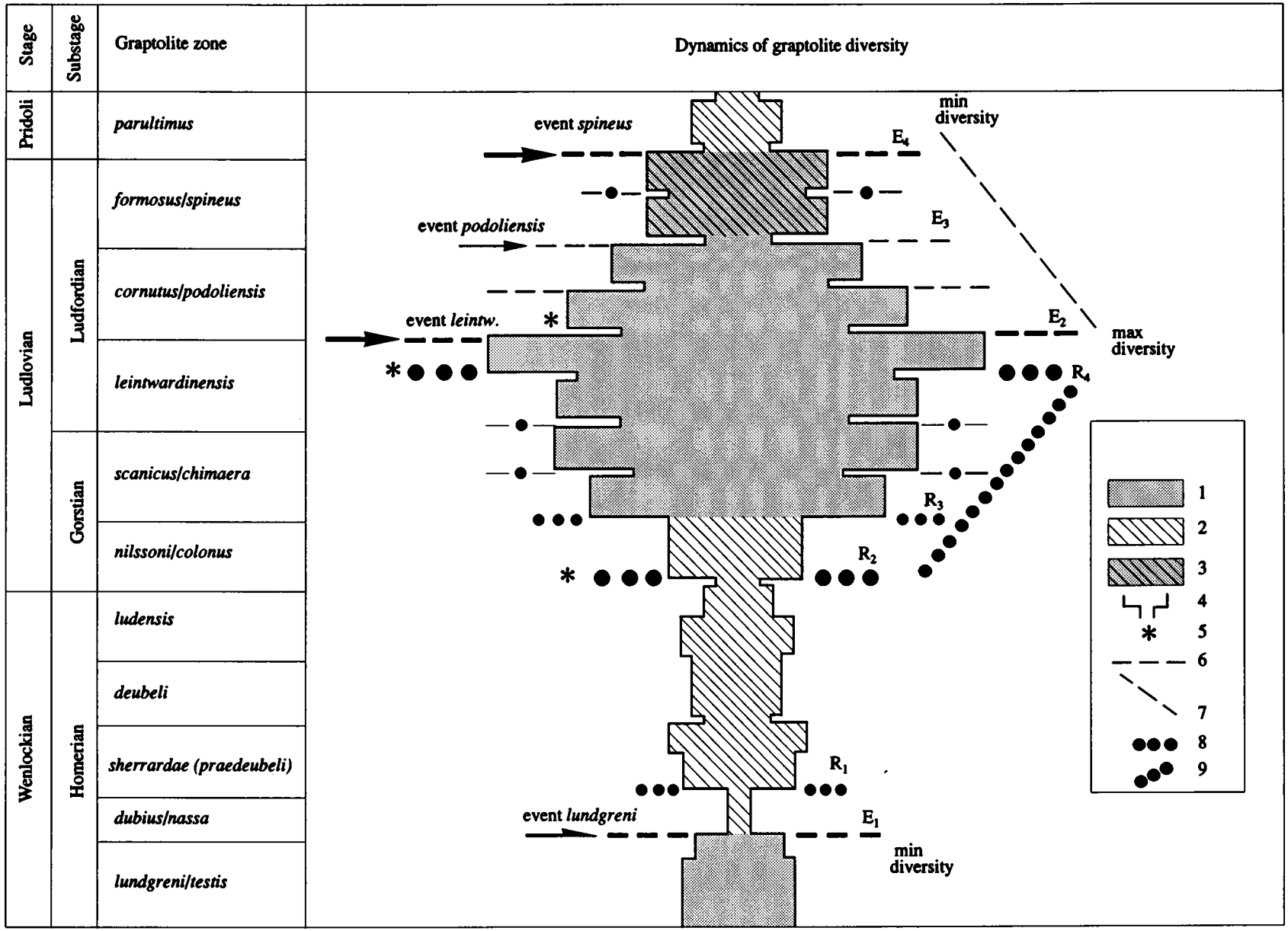

Fig. 4. *Graph of diversity dynamics for the late Wenlockian and Ludlovian monograptids in the sections of the Kursala Formation, Peshkaut Valley, the Alai Range.*
1 - 3 – morphological diversity: 1 – high, 2 – low, and 3 – moderate; 4 – the species diversity; 5 – appearance of the new morphological features; 6 – the extinction levels; 7 – the diversity reduction phase; 8 – the radiation levels; 9 – the diversification phase.

lineage of the *idoneus–sherrardae* at the boundary of the *Ludensis* and *Milssoni–Colinus* zones gives rise to the new Ludlovian faunas of cucullograptid (*Lobograptus*), neocucullograptid (*Bohemograptus*), and linograptid (*Neodiversograptus*). The second late Wenlockian lineage of *praedeubeliludensis* serves as the ancestor for the saetograptid fauna, which, in many sections, dominates in zonal graptolite assemblages of the early Ludlovian. Since the beginning of the *Nilssoni–Colonus* Zone, there has been a splitting into two branches of saetograptid (*S. varians*) and colonograptid (*C. colonus* and *C. roemeri*). The branches develop in parallel up to the beginning of the Ludfordian, inclusive, at the base of divergence and phyletic evolutionary processes. The fauna evolution is characterized by modification of the aperture apparatus in a form of paired lateral lobes of variable shape and by a varying degree of the astogenetic penetration and expression of new morphological features.

Several new morphotypes of monograptids with apertural lobes, consisting of microfusellar tissue (*M. micropoma*), and dorsal hoods, consisting of the common fuselluses (*M. uncinatus*), appear at the beginning of the *Nilssoni–Colonus* Zone. The origin of fuselluses remains cryptogenic. Ancesters of the simultaneously appearing plectograptids (*Plectograptus macilentus*, *Spinograptus spinosus*, and *Holoretiolites*) are unknown so far.

The next radiation phase (Fig. 4, R_3) characterizes the *Scanicus–Chimaera* Zone. The divergence of ancestral lobograptids (*L. progenitor*), the main form of which is the *Lobograptus simplex* (Urbanek, 1966), takes place in a short period of time. Four or five phyletic lines of cucullograptids with symmetrical and asymmetrical apertural apparatus develop during the Gorstian time. These morphs can be differentiated only during study of three-dimensional or well-preserved flat graptolites. The high speciation rate, when the appearing taxa often replace each other in several lineages (*scanicus–expectatus*; *hemiaversus–rostratus*), is typical for the cucullograptids. There are also examples of divergent development (*invertus–cirrifer* lineage). The basic changes are the modifications of the theca apertures at the late astogenetic stages, resulting in the complication and development of secondary asymmetry of the paired lobes. These changes take place in several parallel lineages. The primitive species *Lobograptus*, with bilateral symmetry of apertural apparatus, the species *Lobograptus*, which become asymmetric because of right lobe hypertrophy, as their apertural structures develop, and the species *Cucullograptus*, with acute enlargement of the right lobe dimension, can serve as examples.

The ancient cucullograptid lineage (*B. bohemicus*) remains conservative during the largest part of the early Ludlovian. Only evolutionary microchanges of the aperture form and the sicula dimensions (Urbanek, 1970) take place here. Two independent lineages (*B. bohemicus tenuis* and *B. praecornutus* (Figs. 1 and 2)) appear in the upper part of the *Scanicus–Chimaera* Zone as a result of the divergence of the bohemograptid stem. Monograptids of the *M. uncinatus* group occur rarely and preserve the main plan of apertural structure in a form of the dorso-lateral hood. The taxonomic composition of the graptolite assemblages near the Gorstian–Ludfordian boundary in the Kursala Formation of the South Tien Shan and in the Cape Phillips Formation of Arctic Canada indicate a diversification of monograptids in the lineages *P. dubius* and *M. dalejensis* (Fig. 4, R_4), as is evident by changes of dimensions, contours, and theca proportions. A new morphotype of the *Linograptus posthumus* polydendritic colony, which attains the possibility of producing cladiums from the sicula aperture, appears in the *Leitwardiensis* Zone.

The top of the *Leintwardinensis* Zone coincides with an acute reduction in the taxonomic and morphological diversity of the monograptid fauna (Fig. 4, E_2) and with the entire disappearance of plectograptids in all known sections. A noticeable reduction in the geographic ranges of graptolites can also be observed at this time. For a long time, the final extinction of the Silurian graptolites was related with the disappearance of the *leintwardinensis* assemblage in sections of Great Britain. The latest monograptid fauna of the Ludlovian was discovered in the Barrandien. It was studied in detail using three-dimensional specimens on the volumetric examples from the Melnik and the Siedlec Beds of Poland (Urbanek, 1966, 1970). The extinction event at the top of the *Leintwardinensis* Zone was first interpreted by Urbanek as a deep biological crisis in the Late Silurian history of the group. Tsegel'nyuk (1981) confirmed this conclusion using the large geological collections from the wells of the Volyn' area. The unexpected and synchronous disappearance at the top of the *Leintwardinensis* Zone of many genera, groups, and species (*Plectograptus*, *Saetograptus*, *Colonograptus*, *Lobograptus*, *Cucullograptus*, and others; Koren' 1992) was proved in the sections with uninterrupted paleontological characteristics (the Kursala Formation of the South Tien Shan). Nevertheless, this extinction was selective, because graptolite assemblages became lacking mostly in specialized colonies, which represented the terminal forms of several phylogenetic lines. At the same time, the transit taxa overcame the crisis, resulting in the origin of the late Ludlovian monograptid fauna. Every subsequent event of extinction from the beginning of the *Bohemicus–Kozlovskii* Zone to the end of the Silurian acutely influenced the taxonomic and morphological diversity of graptolites. For example, in the Kursala Formation sections, the assemblage became two times less diverse at the end of the *Leintwardinensis* Zone, three times less diverse after the *podoliensis* event, and seven times less diverse during the last extinction in the *Formosus–Spineus* Zone (Fig. 4). The number of transit taxa also decreases (from 9 or 10 down to 3) during this time.

Neocucullograptids, represented by such genera as *Bohemograptus*, *Neolobgraptus*, *Polonograptus*, and

Neocucullograptus, are the main components of the post-crisis Ludfordian fauna in many regions. They form the basis of the late Ludlovian assemblages in the territories of Poland, Volyn', and South Tien Shan and are represented by some diagnostic taxa in the Kopanina Beds of the Barrandien, being unknown in the coeval assemblages of Arctic Canada and Arctic Russia. The morphological transformations of neocucullograptids took place because of the acquisition and the fastening ability of the colonies to create apertural additions from the microfusellar tissue (Urbanek, 1970). The structure and evolutionary trends of apertural apparatus in the *praecornutus–cornutus* and *auriculatus–kozlowskii* lineages are distinctly different, and both lineages terminate with the highly-specialized *B. cornutus* and *N. kozlowskii* taxa. The development of apertural lobes, which are the most complicated among all the known Silurian graptolites, characterizes the second lineage. Representatives of the *Neocucullograptus auriculatus*, *"Monograptus" egregius*, and *Polonograptus podoliensis* groups are the most widespread among neocucullograptids, being distinguishable in the materials of various preservation. The trend toward forming progressively longer and superimposed thecas during the astogenetic process, rarely noted in the Silurian graptolites, is typical of the two latter groups. The growing length of sicula can be observed in some taxa (*"M." proegregius*). It seems quite probable that both originated from one common ancestor (Urbanek, 1970).

The important elements of the Ludfordian graptolite assemblages in Arctic Canada and the South Tien-Shan are the *M. dalejensis* and *M. uncinatus* groups, untouched by the extinction event at the end of the *Leintwardinensis* Zone (Fig. 1). The first group is connected in its origin with the pristiograptid stem and is characterized by a greater length of all thecas except the outside proximal ones. The second group represents colonies with different astogenetic penetration of the apertural hoods. Change in the dimensions of the apertural structures, reduction of the lateral parts of the hoods, and development of paired lateral lobes, followed by their gradual disappearance (Tsegel'nyuk, 1981) are traceable in the phylogenesis of this group.

The graptolite diversity again reduces acutely as a result of the *podoliensis* extinction event at the end of this species zone (Fig. 4, E). At this time, the neocucullograptid fauna (*Bohemograptus*, *Neocucullograptus*, and *Polonograptus*) terminates its evolution. Some species of the *M. uncinatus* group come to extinction, and the representatives of the *M. dalejensis* group disappear. The species diversity in the *Formosus–Spineus* Zone is noticeably reduced, though a partial replacement of the taxa takes place at this time as a result of the nearly simultaneous appearance of the short-lived *M. balticus*, *M. spineus*, *M. acer*, *M. hamulosus*, *M. formosus*, and other species. The first two species originate, most likely, from monograptids of the *M. uncinatus* group, but the preceding forms of the remaining species remain unknown. All of them are characterized by the high specialization of theca and its aperture, which was attained by different ways, such as modification of the apertural hoods, appearance of lateral lobes and spines, length increase, bending, or partial isolation of the theca. The species of the *M. uncinatus* group, including *M. bessobaensis*, *M. caudatus*, and *M. rectus*, again become highly important in assemblages of the *Formosus–Spineus* Zone. They are distinctive by the rather stable rhabdosome structure, by only minor differences in the dimensions of the apertural hoods, and by the degree of reduction of their lateral parts. The *P. dubius* group refers to the transit taxa. Some of its species (*P. fragmentalis*) show an outburst in abundance well-marked in the European (Kříž *et al.*, 1986) and the South Tien Shan sections.

The extinction at the end of the *Formosus–Spineus* Zone (Fig. 4, E) terminates the evolution of the late Ludlovian monograptids. This is not unexpected, but has a stepwise character in comparison with the previous *leintwardinensis* and *podoliensis* events. For example, the *M. hamulosus* and *M. latilobus* species disappear within the zone, and *M. spineus* and *P. fragmentalis* continue to exist to the end of the zone, whereas the *M. formosus* passes across the Ludlovian–Pridolian boundary, though the diversity of its populations is acutely reduced in the *Parultimus–Ultimus* Zone. The spineus event terminates all specialized lineages of monograptids. The colonies with a simple theca structure and a paired lateral rise on the apertures in the proximal part or within the entire colony, are found to be the most successful ecologically. Such forms are *M. latilobus*, which existed throughout almost the entire Ludfordian, and *M.* sp. nov. aff. *latilobus* and *M. rarus*, which appeared at the end of the *Formosus–Spineus*, Zone. The early Pridolian species (*M. parultimus*, *M. ultimus*, and *M. transgradiens*) most likely originated from them, though direct morphological transitions have not been traced even in the most complete sections. For example, the replacement of the assemblage *Formosus–Spineus* and the *Parultimus* zones in the Kursala Formation of the South Tien-Shan occurs in the monotonous argillites, with a thickness of several centimeters.

The analysis of the diversity dynamics of the Ludlovian graptolite showed that the extinction events had often disturbed the stasis of pelagic communities and mainly defined the trends and character of the following morphological changes. They resulted in the development of associations of low diversity and produced frequent bursts in the abundance of single relic or newly originated taxa in the populations. The new morphological structures, which induced the processes of adaptive radiation, appeared usually in the post-crisis intervals.

Conservative long-lived stems (*Pristiograptus dubius*, *Monograptus uncinatus*, and *Bohemograptus bohemicus*) had the highest evolutionary potential. New lineages developing predominantly toward a higher specialization of the colony originated their

base as a result of underactive evolution or divergence. Morphological changes took place under the stiff evolutionary model of the monograptid colony and concentrated mostly on metatheca and its apertures, testifying to their adaptive nature. New features appeared at the initial or final stages of the astogenesis and were not always spread over the entire colony. There were also gomeomorphic structures in the lineages, strongly divergent relative to the ancestral stem.

The high rate of species origination and the background extinction were typical for the Ludlovian graptolites, and this was expressed in a frequent replacement of morphoecological types in the consequently developing communities. Apparently, the reverse correlations of the diversity level of the synchronous plectograptid and monograptid faunas indicate different adaptive reactions of colonies with reticulate and complete periderm to the same ecological reorganizations.

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Flora of the Kungurian Stage of the Middle Cis-Urals and Its Correlation with the Central Angaraland Floras

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Abstract – The history of the study and the taxonomic composition of the Kungurian flora in the Middle Cis-Urals, which are especially important for paleontological characteristics of the Kungurian and for the determination of its boundaries in other regions, are discussed in this article. The Kungurian Stage of the stratotype area is correlated with the Ishanova Horizon of the Kuznetsk basin and its analogs using a number of common taxa. Thus, the boundary between the Permian series in the Siberian sections ought to be placed essentially lower, compared with its traditional position.

Flora characterizing the Kungurian deposits in the stratotype area (the Middle Cis-Urals, Permian Region, and the Sylva River basin to the east of Kungur Mountain) is very interesting because of its original and diverse taxonomic composition, and because of its stratigraphic and paleophytogeographical position. Unfortunately, it remains poorly studied up to the present, which makes difficult its comparison with both the adjacent floras of the Subangaraland ecotone belt and the more remote Permian floras of Central Angara land.

The more precise definition of paleontological boundaries of the Kungurian requires the study of the Kungurian flora of the Middle Cis-Urals. The uppermost of them is at the same time a boundary between the series of the Permian System(!). The fauna is poor in the Kungurian stratotype area (Stepanov *et al.*, 1984), but it occurs together with abundant plant remains. The terrigenous rocks, best characterized paleontologically by floral remains, belong to those Permian deposits of other regions, which are usually correlated with the Kungurian Stage of the Middle Cis-Urals. The Rotliegende and Zechstein of West and Central Europe and the Upper Balakhonka beds and their analogs in Siberia represent such deposits. These facts, together with the absence of effective alternative methods, raises the significance of the Kungurian flora in solving the stratigraphic problems. At the same time, its phytogeographic position between two main Permian phytochories of the Northern Hemisphere (Euramerican and Angaraland) and, as a result, the presence of both the typical Angaraland and Euramerican elements in its composition make it quite important in solving not only stratigraphic but also paleobiographic enigmas.

In this article, I consider a history of the study of the Kungurian flora of the Middle Cis-Urals, its taxonomic composition, and the problems of paleobotanic correlation of the Kungurian Stage with the strata of similar age in the Central Angaraland (the Kuznetsk basin).

HISTORY OF STUDY OF THE KUNGURIAN FLORA IN THE MIDDLE CIS-URALS

S.S. Kutorga (1838, 1844), E.I. Eikhvald (1854, 1861), R. Ludwig (1863), and some other paleontologists of the last century described the first samples with plant remains of the Lower Permian in the Middle Cis-Urals, including the Kungurian deposits. Unfortunately, the materials were mainly collected only occasionally without exact geographical labelling and age dating. Only in the 1930s did M.D. Zalessky (1932, 1933, 1934, 1937, 1939a, 1939b) publish numerous and rather detailed descriptions of plant remains of the Kungurian Stage of the western Urals and the Cis-Urals, which are now somewhat out of date. Zalessky proposed the name "Bardian flora" (after the Barda River in the Sylva River basin), widely used in the paleobotanic literature. The postwar plans of the scientist included special study of the Bardian flora (Lapo and Fisunenko, 1987), but his premature death prevented their realization. The collection, described by Zalessky, was prepared mostly by collector–paleontologist G.T. Mauer, who was at that time a chief in the Department of Nature in the Perm Regional Museum. The Kungurian plants (*Mauerites* Zal. and *Bardia mauerii* Zal.) and insects (*Permoscytinopsis mauerisformis* G. Zal, *Maueria* G. Zal., and others) have been named in his honor.

S.V. Meyen, the outstanding Russian paleobotanist studied the Bardian flora conifers (Meyen, 1986, 1990a), original dicranophylls (Meyen, 1969), and some pteridosperms (Meyen, 1982, 1983) at the modern level. L.V. Glukhova (1984a, 1984b, 1989) published data on the epidermal structure of cordaits and cordait-shaped plants of the Kungurian Stage of the

Middle Cis-Urals. At the same time, the work of V.P. Vladimirovich (1985) appeared, which was organized as a catalog of main occurrences of the Bardian flora plants. I.A. Ignatiev (1988) proposed a new original interpretation of one endemic form of the Middle Cis-Urals Kungurian flora: the *Pholidophyllum ornatum* Zal. I studied a variation and a callipterid epidermal structure of the Bardian flora, the *Rhachiphyllum* (al. *Callipteris*) *retensorium* (Zal.) Naug. The first data on the structure of their generative sphere (Lopadiangium sp. SVN-1) was obtained and the data on morphology and taxonomy of the Bardian psygmophylloids and ginkgo trees(?) [*Psygmophyllum expansum* (Brongn.) Schimp., *P. cuneifolium* (Kutorga) Schimp., *Palaeoginkgomacroloba* gen. et sp. nov. (in prep.)] were generalized. At the same time, some nomenclature problems were resolved (Naugol'nykh, 1991, 1991a, 1991b; Kerp *et al.*, 1991).

THE TAXONOMIC COMPOSITION OF THE BARDIAN FLORA OF THE KUNGURIAN IN THE MIDDLE CIS-URALS

The Bardian flora is, undoubtedly, one of the richest and most original among all the Permian floras of the Northern Hemisphere and, probably, of the whole Earth. At present, it includes about 100 genera and 200 species of land plants. Apparently, these figures reflect only indirectly the real taxa diversity of the Bardian flora, which was, most likely, much higher. Even now, I have remains of vegetative and generative organs of the Bardian plants in my collection, which still have not been studied in detail, but which evidently belong to a new species or even genera. At the same time, many taxa determined earlier and described in accordance with the "leaf" paleobotanic monotype–typological conception of the lowest taxa need serious revision. Thus, for example, the synonymy of species nomens among some Kungurian *Pecopteris*, *Mauerites*, *Rhachiphyllum* (al. *Gallipteris*), *Psygmophyllum*, and others appears to be quite probable. It is impossible to resolve this problem unambiguously, because the type specimens of many taxa determined by Zalessky were lost (Krishtofovich, 1949).

The lower plants from the Kungurian flora of the Middle Cis-Urals are known in several remains of doubtful nature, previously determined by me, such as the thallus remains of aquatic macrophytes referred to *Chlorophyta* or *Phaeophyta* (?).

The Bardian flora bryophytes are known from the description of the only specimen (Zalessky, 1937) of *Marchantites lorea*, attributed by Zalessky to liveworts (*Hepaticopsida*).

The pteridophytes, presenting about one-fourth of the whole species diversity of the Bardian flora, are subdivided into three classes: Equisetopsida, Lycopodiopsida, and Polypodiopsida (in this work, the system of highest taxa of plants proposed by Meyen (1987) is assumed). The equisetopsids are the most diverse among them, being represented by about 25 species. The Bardian ferns include approximately 15 - 20 species, and the rare lepidophytes, 1 or 2 species.

The Kungurian arthropsids from the Middle Cis-Urals (Plates I, 1, 6; II, 1, 5 - 8) are known mostly by vegetative leaf-bearing shoots, more rare, by large trunks up to 10 - 20 cm in diameter (*Calamites gigas*). In exclusively rare cases, the fructifications of arthropsids (strobiles, fertile zones, or individual sporangiophores) may be encountered.

One can refer the Bardian arthropsids remains to two orders: Bowmanitales (Bowmanitaceae family, the *Bowmanites* and *Sphenophyllum* genera) and Calamostachyales (Calamostachyaceae family, the *Calamites* and *Annularia* genera). Sterile shoots of phyllothecas and *Phyllotheca*-like plants of the Bardian flora in association with fructifications of the *Equisetinostachys* type are attributed, most likely, to the third order of Equisetales.

The arthropsids include a large number of endemic forms peculiar only to the Bardian flora at both the species and genus levels. The *Sachyogyrus*, *Corynophyllites*, and *Equisetina* are typical representatives of the endemic genera. The species of the latter genus were indicated earlier for the Carboniferous and Permian of the central region of Angaraland (Rasskazova, 1961; Radchenko, 1956; Khakhlov, 1964; and others). Later, however, Meyen (1971, 1990b) showed that Siberian plants belonged to the *Phyllotheca* genus. The list of endemic species is more substantial: *Bowmanites biarmensis* Naug. sp. nov. (in prep.), *Sphenophyllum biarmicum* Zal. (Plate II, 7), *Sachyogyrus multifarius* Zal., *Phyllotheca biarmica* Zal. (Plate II, 5 - 6), *P. campanularis* Zal. emend. Naug. emend. nov. (in prep.; Plate I, 6), *P. amphora* Naug. sp. nov. (in prep.), *P. stenophylloides* Zal., *P. scyphulifera* Zal., *P. stellifera* Zal., *P. bardensis* Zal., *P. macrostachya* Zal., *P. peremensis* Zal., *Corynophyllites setiformis* Zal., and *Paracalamitina ignatievii* Naug. sp. nov. (in prep.; Plate II, 8). I doubt the validity of some of the above-listed taxa, especially those whose description of the only specimens are known only from the literature. Nevertheless, the Bardian equisetaceous plants are generally very peculiar and present the clearest feature of the flora as a whole.

The ferns occur considerably more rarely and are still poorly studied. They are known mainly from remains of sterile leaves of the endemic species of the *Pecopteris* and *Sphenopteris* genera. I discovered fern leaves of at least two more genera: *Prynadaeopteris* and *Ovopteris* (Plate II, 3). The new data on fructification of the Bardian ferns indicates that they are more diverse than was reported earlier [the *Orthotheca* (Plate I, 4), *Ptychocarpus*, *Oligocarpia*, and *Discopteris* genera and others].

Lepidophytes are very rare in the Bardian flora. At present, only their isolated phyllodes (*Viatscheslaviophyllum sp.*) and the decorticated trunk fragments "*Knorriopsis*" of dendrite lepidophytes, most likely of the *Viatscheslavia-Signacularia* type, are known.

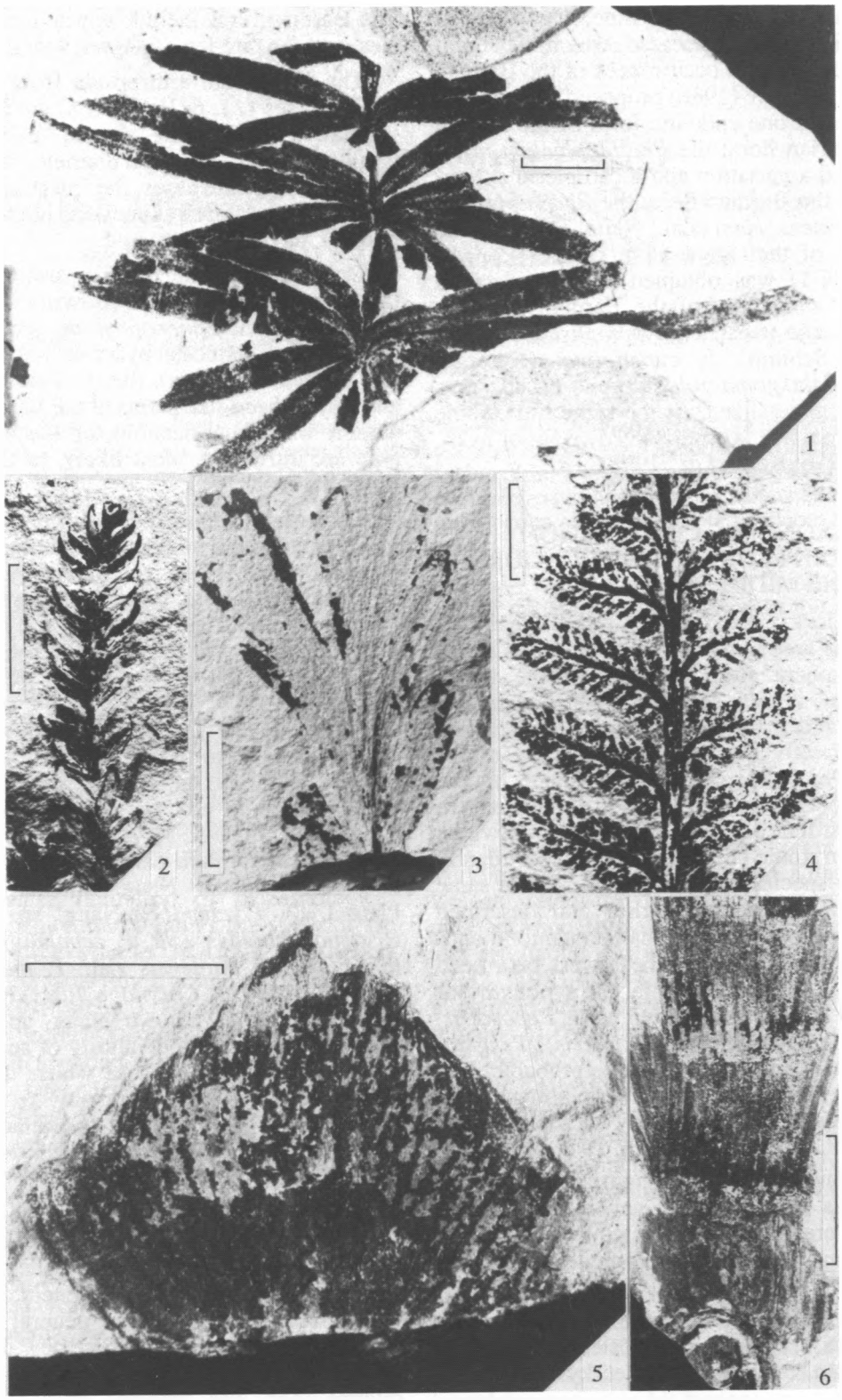

Plate I. *Kungurian flora in the Middle Cis-Urals.*

1 – *Annulina neuburgiana* (Radcz.) Neub., N 3737/46; 2 – *Taxodiella* (al. *Walchia*) *bardaeana* (Zal.) *S. Meyen*, N 3773(11)/296(91); 3 – *Psygmophyllum expansum* (Brongn.) Schimper, N 3773(11)/96(89); 4 – *Orthotheca* sp. (sp. nov.?), N 3773(11)/291(91); 5 – *Nephropsis* cf. *rhomboidea* Neuburg, N 3773(11)/311(91); 6 – *Phyllotheca campanularis* Zal., N 3773(11)/262(91).

The Middle Cis-Urals, Perm' region, left bank of the Sylva River downstream of the Chekarda River mouth; "Chekarda-1" locality. The Koshelevo Formation, the Iren' Horizon, the Kungurian Stage. The length of the scale line is 1 cm.

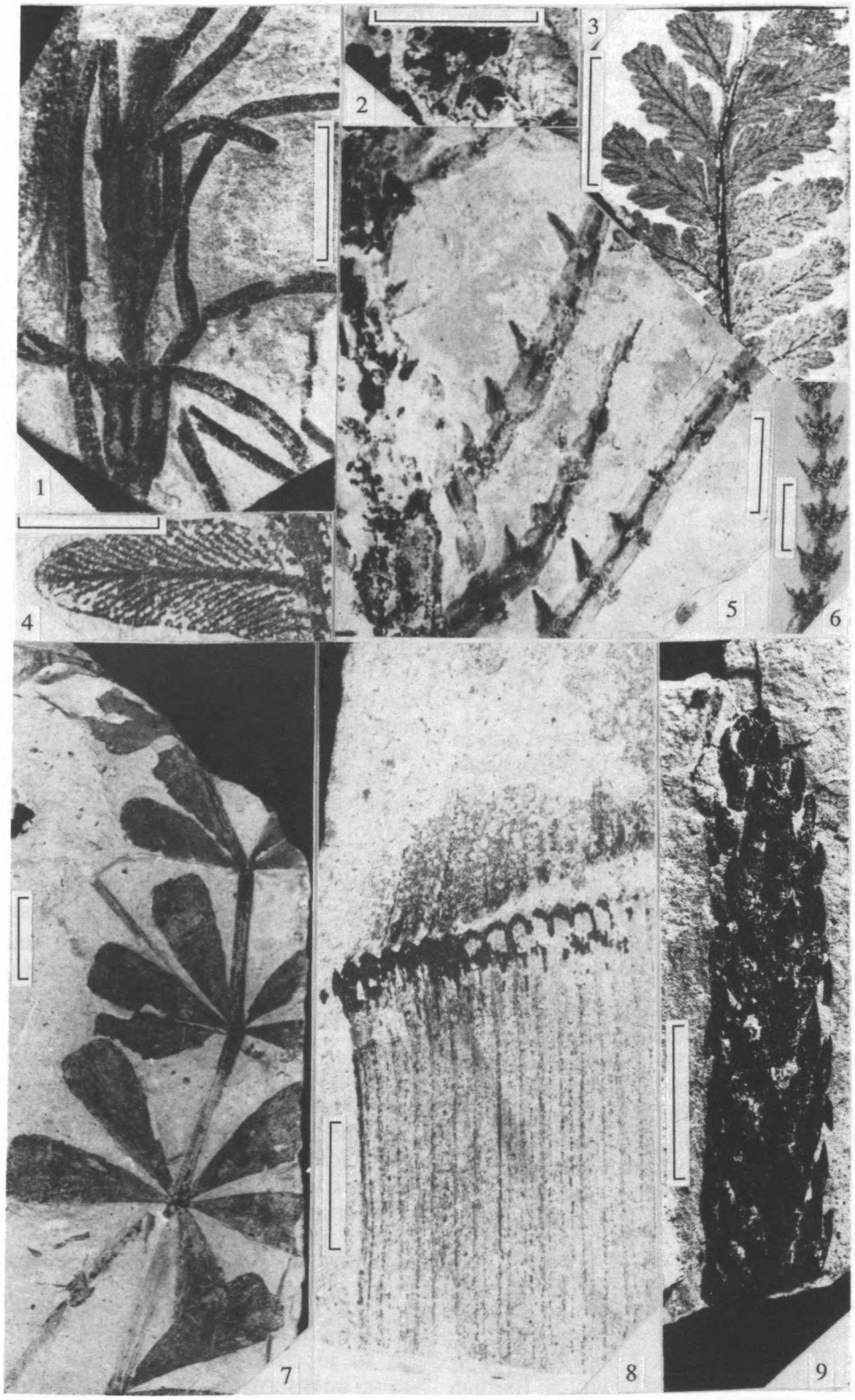

Plate II. *Kungurian flora in the Middle Cis-Urals.*

1 – *Phyllotheca* sp. SVN-1 (in prep.), N 3773(11)/290(91); 2 – *Lopadiangium* sp. SVN-1, N 3773(11)/61(89); 3 – *Ovopteris* sp., N 3773(11)/288(91); 4 – *Rhachiphyllum* (al.*Callipteris*) *retensorium* (Zal.) Naug., N 3737/72; 5 – *Phyllotheca biarmica* Zal., N 3773(11)/108(89); 6 – *Phyllotheca biarmica* Zal., N 3773(11)/191(89); 7 – *Sphenophyllum biarmicum* Zal., N 3737/14; 8 – *Paracalamitina ignatievii* Naug. sp. nov. (in prep.), N 3773(11)/87(89); 9 – *Cyparissidium* (al. *Walchia*) *appressum* (Zal.) S. Meyen, N 3773(11)/26(89).

The Middle Cis-Urals, Perm' region, left bank of the Sylva River downstream of the Chekarda River mouth; "Chekarda-1" locality. The Koshelevo Formation, the Iren' Horizon, the Kungurian Stage. The length of the scale line is 1 cm.

Gymnosperms compose three-fourths of the Kungurian flora species from the Middle Cis-Urals. They are also very original, in spite of having a number of taxa common with Central Angaraland flora. The callipterids and the psygmophylloids among Pinophyta (the Peltaspermales order of the Ginkgoopsida class) and conifers, with original structural features lacking specimens from other regions this order, are the most typical Bardian forms.

The callipterids are common in the majority of the Bardian flora localities and are represented by several genera: (1) *Rhachiphyllum* (al. *Callipteris*) (Plate II, 4), *Comia* (leaves); (2) *Lopadiangium* (Plate II, 2) (female fructifications); and (3) *Permotheca*, *Asterodiscus* (male fructifications). The *Sylvia* and *Sylvopteris* endemic genera with simple-pinnate fronds are similar to the callipterids in their form of pinnules and structure of rachis. The psygmophylloids (Trichopityaceae? family) are also widely represented by the "leaves" genera (*Psygmophyllum* (Plate I, 3) and *Bardia*). The *Mauerites* with the associated fructifications of *Biarmopteris* (Trichopityaceae family; Meyen, 1982, 1983) are similar to psygmophylloids in general morphology. Descriptions of other pteridophylls of unclear taxonomic affiliation, part of which probably belongs to peltaspermaceous, are known from the literature (Zalessky, 1937, 1939a, 1939b).

The Bardian flora is traditionally considered rich in different "ginkgophytes." Usually, they are recognized as various psygmophylloids, which belong to the Peltaspermaceae, rather than to the true Ginkgoaceae. Two *Baiera*like plants, *Uralobaiera* and *Biarmobaiera*, described by Zalessky (1939a), require additional study. The new endemic monotype *Palaeoginkgo* genus determined by me, but still not characterized effectively, seems to be of the Ginkgoales order, and, most likely, of the Ginkgoaceae family.

The Kungurian cordaits from the Middle Cis-Urals flora (Pinopsida order, Cordaitanthales class) are represented by all three families – Cordaitanthaceae, Vojnovskiaceae, and Rufloriaceae – and have many common features with typical Angaraland representatives of the order. They consist predominantly of mutual genera (*Rufloria*, *Angophyllites*, *Sparsistomites*, *Nephropsis* (Plate I, 5), *Crassinervia*, *Lepeophyllum*, and *Gaussia*), though the endemics (*Pholidophyllum*) are present as well.

The specimens of the Dicranophyllales order (*Entsovia* and *Meristophyllum* genera) compose an interesting group of Bardian plants, known also from the Pechora province of the Cis-Urals. The *Dicranophyllum* genus was earlier cited in the list of typical Bardian plants (Zalessky, 1934, 1937, 1939a), but the cases at hand were rather the leaves of Peltaspermaceous pteridosperms of the *Mauerites* or *Psygmophyllum* ex gr. *cuneifolium* type.

The kungurodendroid conifers [Pinales order, Lebachiaceae (= Lebachiellaceae) family, Kungurodendroidea subfamily], the abundance of which makes the flora on the whole similar to some Lower Permian floras of the European Rotliegenden along with dominating conifers (Kerp *et al.*, 1990), are an important element of the Kungurian flora in the Middle Cis-Urals. Among them are the remains of the *Kungurodendron* genera, whose leaf-bearing sterile branches are classified as *Walchia* or *Cyparissidium* forms (Meyen, 1986; Plate II, 9). *Concholepis* (according to my data) and *Bardospermum* (Meyen, 1990a) are the most typical. The shoots of the *Taxodiella* (al. *Walchia*) *bardaeana* (Zal.) S. Meyen (Plate I, 2), fructifications of which still remain unknown, are also not rare. In addition, conifers of the genera *Voltzia*, *Ullmania*, and *Brachiphyllum* occur usually in the lists of the Bardian flora, but the validity of the determination of these genera is in doubt. Trunks of the Bardian conifers, sometimes large enough (up to 10 cm in diameter and with hems of branches fallen off), are attributed to the *Tylodendron* genus. The *Ammatopsis* and *Bardella* genera proposed by Zalessky are, apparently, geterotype synonyms of *Bardospermum*, being defined on the sterile shoot remains.

The isolated seeds of gymnosperm plants of the Kungurian flora in the Middle Cis-Urals are quite diverse (Fig. 1 - 4). A large number of genera and even species(!), common both to the adjacent Pechora basin and the remote regions of Central Angaraland, are presented here in addition to the endemic *Craspedosperma*, *Uralosperma*, *Permosperma*, and *Thysanosperma*, which opens broad possibilities for interregional correlations. The seeds of some cordaits presumably of the genera *Sylvella*, *Bardocarpus*, *Samaropsis*, and *Cardiocarpus*, and the seeds of Peltaspermaceae?, *Cordaicarpus* and *Carpolithes* forms, belong to taxa mutual with those of the other Siberian regions.

A large number of plants of unclear taxonomy (*Xiphophyllum*, *Adrophyllum*, *Listrodium*, *Sphegophyllum*, *Calleophyllum*, *Sphegopteris*, and other genera) occur in the Bardian flora in addition to the above-listed taxa. The material presently at my disposal does not clear up their nature.

In his works, Zalessky (1933, 1937, 1939a) described and presented among the typical Bardian plants leaves identified as new species of the *Glossopteris* and *Gangamopteris* genera (Glossopteridales or = Arberiales orders). To me it seems that Zalessky made a mistake: he described isolated anomalous large leaves of the *Sphenophyllum* sp. SVN-1 (in prep.) type. Folds of the leaf plates could be taken erroneously as anastomoses between the veinlets.

PROBLEMS OF CORRELATION OF THE KUNGURIAN STAGE AND SYNCHRONOUS DEPOSITS OF CENTRAL ANGARALAND (THE KUZNETSK BASIN)

I attempted to define heterogenous ingredients of the Kungurian flora from the Middle Cis-Urals at the genus level (Fig. 5). The main part (39%) of the general

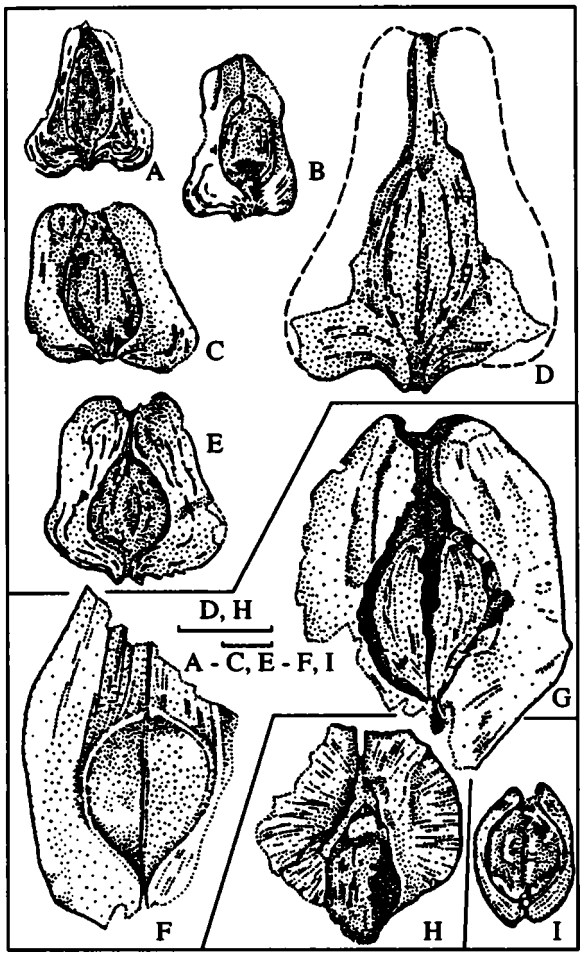

Fig. 1. *The seeds of gymnosperm plants from the Kungurian Stage of the Middle Cis-Urals.*

A - E – *Samaropsis triquetra* Zalessky. A – 3773(11)/117(89), B – 3737/229a, C – 3737/79, D – 3737/157, E – 3773(11)/168a(89). F - G – *Samaropsis danilovii* Suchov. F – 3737/201, G – 3737/274; H – *Samaropsis* ex gr. *erunakovensis* Radcz. vel *irregularis* Neub., H – 3737/231; I – *Samaropsis subpatula* Suchov, I – 3737/163. Middle Cis-Urals, Perm region, the left bank of the Sylva River downstream of the Chekarda River mouth; the locality "Chekarda-I." The Koshelevo Formation, the Iren' Horizon, the Kungurian Stage. The length of the scale line is 2 mm.

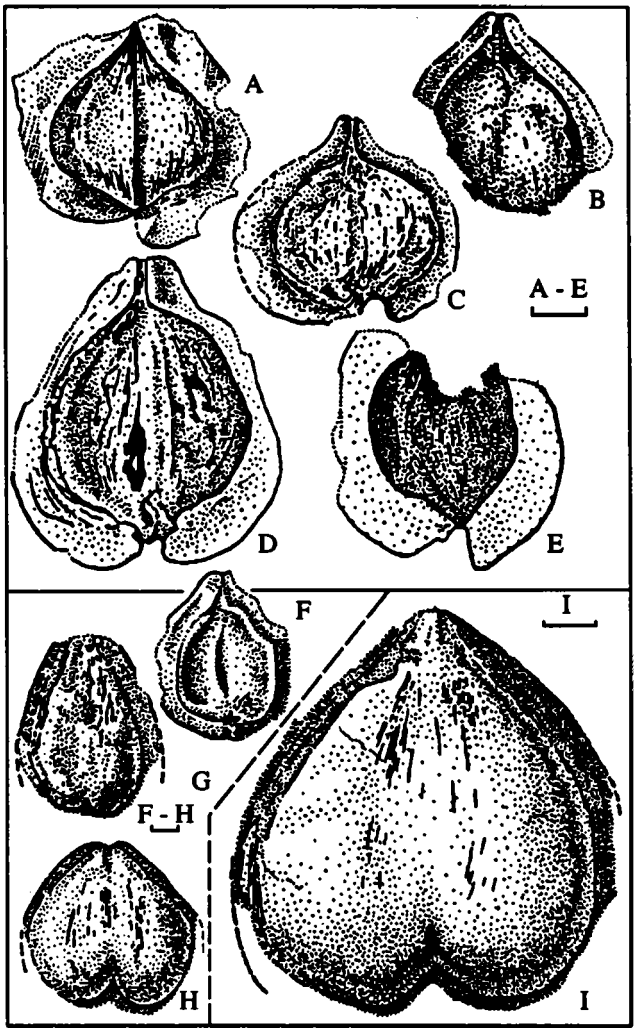

Fig. 2. *The seeds of gymnosperm plants from the Kungurian Stage of the Middle Cis-Urals.*

A - E – *Samaropsis tuberculata* Dombrovskaya. A – 3737/250, B – 3737/232, C – 3737/101, D – 3737/203, E – 3737/233. F - I – *Cardiocarpus cordatus* (Eichwald) Schmalhausen. F – 3737/230a, G – 3737/140, H – 3773/183a, I – 3737/203. Middle Cis-Urals, Perm region, the left bank of the Sylva River downstream of the Chekarda River mouth; the locality "Chekarda-I." The Koshelevo Formation, the Iren' Horizon, the Kungurian Stage. The length of the scale line is 2 mm.

taxonomic composition falls to the endemic genera; plants, similar to Euramerican, occupy 16.5%; the same proportion belongs to the pandemic taxa; 28% shared genera common for the Bardian and typical Lower Permian floras of the Kuznetsk basin. I did not compare the Kungurian flora of the Middle Cis-Urals or of the Vorkuta locality in the Pechora Basin, as such an investigation had been completed already (Vladimirovich, 1986; and others).

I compiled a list of the plant species common to the Bardian flora and Permian floras of the Kuznetsk basin. A number of taxa – *Annulina neuburgiana*, *Prynadaeopteris* sp., *Samaropsis* ex gr. *erunakovensis-irregularis*, *S. danilolovii*, *S. tuberculata*, *S. subpatula*, *Carpolithes globosus*, and *Gaussia* sp. – were identified for the first time in the Kungurian of the Middle Cis-Urals. The position of these species in the Kuznetsk basin sections was traced on the published data (Betekhtina and Sukhov, 1968; Sukhov, 1969; Glukhova, 1984a, 1984b; Meyen, 1982, 1990a; and others). The results are presented in a table of stratigraphic distribution of such taxa as compared with the same or similar forms from the Kungurian of the Middle Cis-Urals (Table 1). An interesting regularity was discovered: a considerable amount of taxa (especially for the isolated seeds and leaves of cordaids) seems to correlate the Kungurian Stage of the stratotype area not

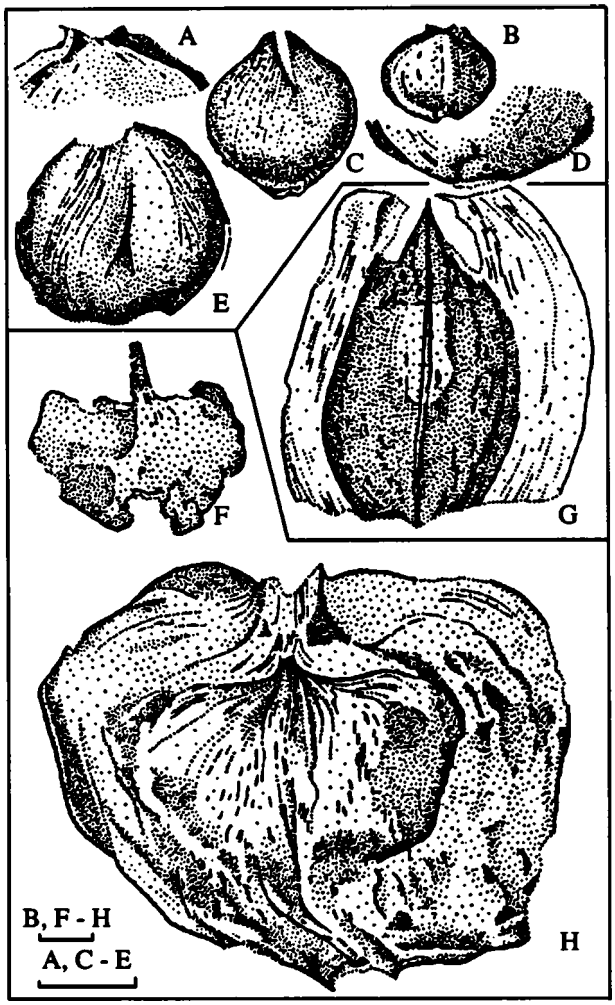

Fig. 3. *The seeds of gymnosperm plants from the Kungurian Stage of the Middle Cis-Urals.*

A - E – *Carpolithes globusus* Suchov. A, B, D – 3737/180; C – 3737/139; E – 3737/141. F – *Bardocarpus* sp., 3773(11)/147-(89)h. G – *Samaropsis* sp., 3737/151. H – *B. superus* Neuburg, 3737/225.

Middle Cis-Urals, Perm region, the left shore of the Sylva River downstream of the Chekarda River Mouth; the locality "Chekarda-I." The Koshelevo Formation, the Iren' Horizon, the Kungurian Stage. The length of the scale line is 2 mm.

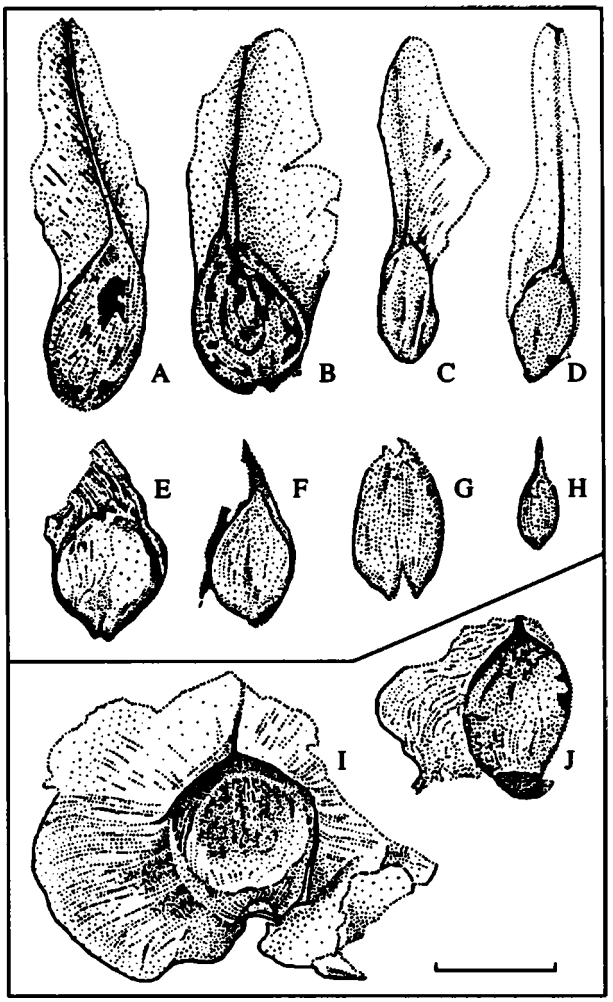

Fig. 4. *The seeds of gymnosperm plants from the Kungurian Stage of the Middle Cis-Urals.*

A - H – *Sylvella alata* Zalessky. A – 3773(11)/199(90); B – 3737/277; C – 3737/11; D – 3737/8; E – 3737/28; F – 3737/84; G – 3737/10; H – 3737/189. I - J – *Samaropsis* sp. (aff. *dombrovskae* Vlad.). I – 3737/100a; J – 3737/145.

Middle Cis-Urals, Perm region, the left shore of the Sylva River downstream of the Chekarda River Mouth; the locality "Chekarda-I." The Koshelevo Formation, the Iren' Horizon, the Kungurian Stage. The length of the scale line is 2 mm.

with the traditional correlatives of the Kuznetsk basin (the Usyatskoe and/or Kemerovo horizons), but with underlying deposits (the Ishanova Horizon). It should be noted that the species of disperse seeds, which are peculiar to the "upper Lower Permian" in Siberia (i.e., the Kungurian, according to Sukhov, 1969) (*Skokia elongata*, *Samaropsis gorbiaczinensis*, *S. pseudoelegans*, *S. dixonovensis*, *S. neuburgae*, *Sylvella elongata*, *Tungussocarpus subtychtensis*, *T. budnikovii*, *Condomajella baranovii*, and *Carpolithes condomaensis*) have not been recognized so far in the Kungurian stratotype of the Middle Cis-Urals. In my opinion, the upper (possibly event) boundary of the Kungurian is well-traced in the Kuznetsk basin. The lower boundary is less defined, partially because of the poorly studied (in the paleobotanic sense) Filippovskoe Horizon in the Middle Cis-Urals. The other Kuznetsk basin species included in Table 1 (mostly not common, but similar to the Bardian species), do not contradict the correlation of the Kungurian stratotype with the Ishanova Horizon, because they have a stratigraphically wider range, though their taxonomic identity with the Kungurian species of the Middle Cis-Urals is not evident.

It is necessary to note that indirect proposals to shift lower the boundary between the Permian series in Siberia (i.e., the upper boundary of the Kungurian Stage) were made already. For example, L.V. Glukhova noted that "as a whole, the Kungurian ruflorians assemblage is similar to the Ishanova one. Both are characterized

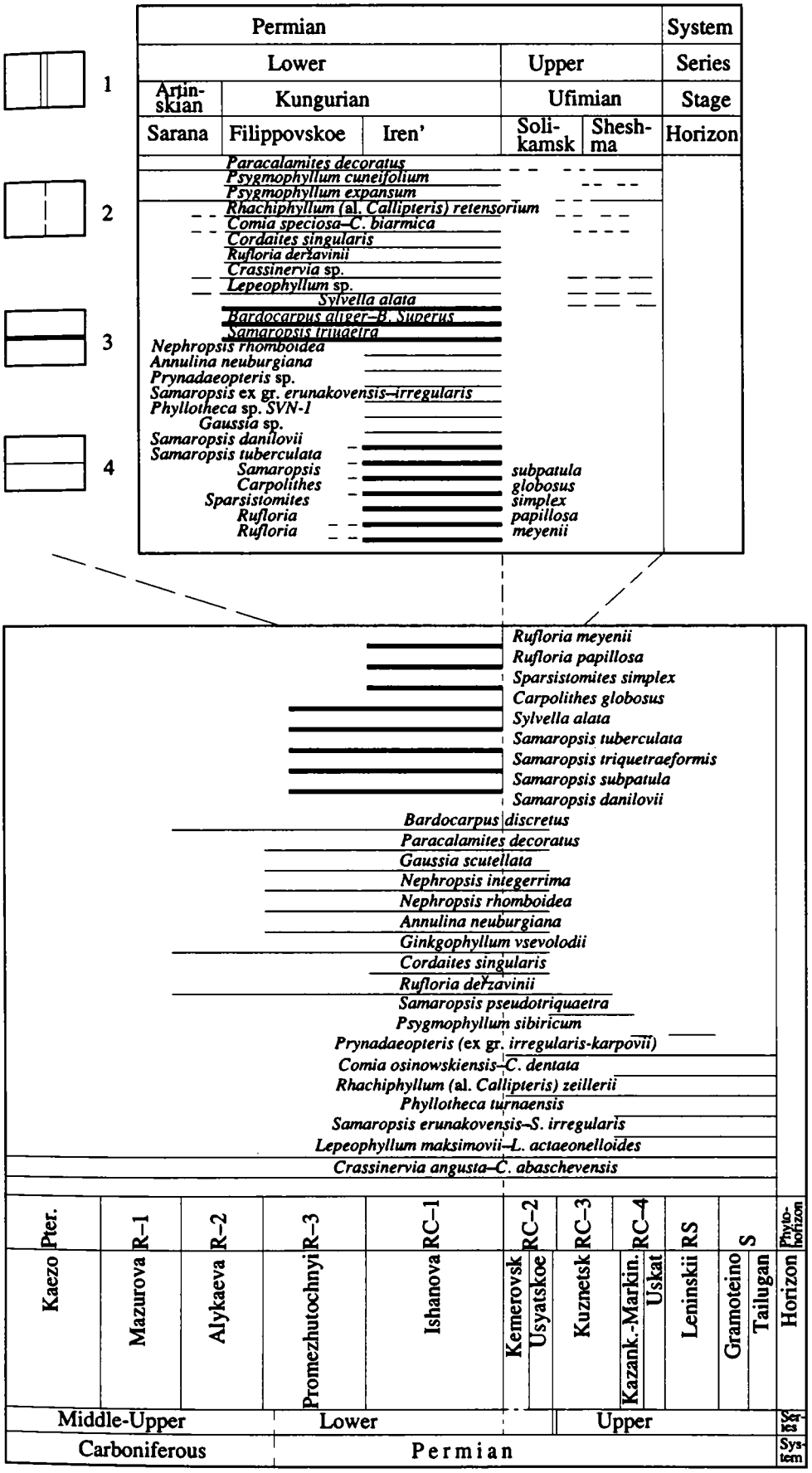

Table 1. *Stratigraphic ranges of taxa, common for the Kungurian Stage of the Middle Cis-Urals (stratotype area) and the Central Angaraland deposits close in age (the Kuznetsk basin)*

1 – traditional position of the boundary between the Permian series in the Kuznetsk basin; 2 – proposed position of the boundary between the Permian series in the Kuznetsk basin; 3 – species of narrow stratigraphic range, well identified both in the Kuznetsk basin and in the Cis-Urals; 4 – species of wide stratigraphic range or determined in open nomenclature

Distribution of the *Annulina neuburgiana*, *Prynadaeopteris* sp., *Phyllotheca* sp. SVN-1, *Samaropsis* ex gr. *erunakovensis-irregularis*, *S. danilovii*, *Gaussia* sp., *Samaropsis tuberculata*, *S. subratula*, and *Carpolithes globusus* Kungurian taxa from the Middle Cis-Urals is given according to the author's data; the rest of the data are cited according to Betekhtina and Sukhov, 1968; Sukhov, 1969; Glukhova, 1984a, 1984b, 1989; Meyen, 1982; Vladimirovich, 1986; and Meyen, 1990a. The names of the phytohorizons and their correlation with the horizons of the stratigraphic scheme for the Kuznetsk basin are given according to Durante and Meyen (Meyen, 1982).

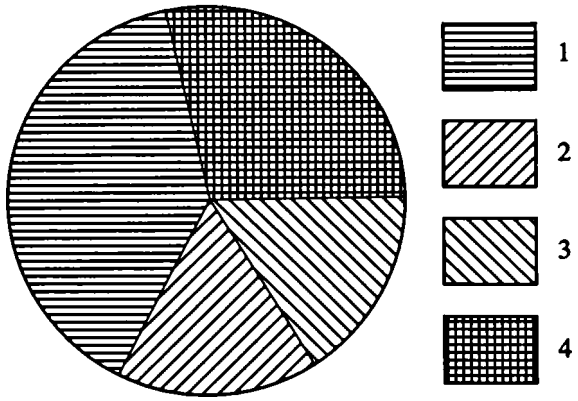

Fig. 5. *The Kungurian flora of the Middle Cis-Urals (the Bardian flora): proportions of genera.*
1 – endemic (39%); 2 – common with the Permian Euramerican flora (16.5%); 3 – cosmopolitan (pandemic) (16.5%); 4 – common with the Central Angaraland flora (28%).

by a combination of ruflorians, having dorsal furrows with cords (*R. papillosa* and others), and ruflorians also having furrows, but without cords (*R. meyenii*, *R. deržavinii*, and *R. unica*). In the Kuznetsk basin, the ruflorians with dorsal furrows and cords do not pass into the overlying Kemerovo-Usyatskoe beds" (Glukhova, 1984b).

CONCLUSION

The Bardian flora from the type sections of the Kungurian Stage in the Middle Cis-Urals is generally endemic (39% of genera are of this type), but it must be included into the composition of the Angaraland phytochory (Subangaraland ecotone belt) because of the presence of a large amount of Angaraland elements (28%). The Kungurian Stage is well correlated with the Ishanova Horizon of the Kuznetsk basin, as is indicated by a number of common taxa. Thus, the boundary between the Permian series in the Kuznetsk basin and, most likely, in Central Angaraland as a whole ought to be lowered significantly, compared with its traditional position.

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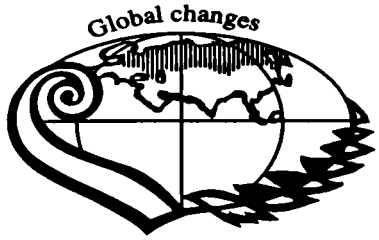

Evolution of the biosphere

A Paleobotanical Basis for the Zonal Subdivision of Continental Plant-Bearing Beds (Upper Permian of the Pechora Basin and Cis-Urals as an Example)

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Abstract – The term *plant-associations zones* is introduced as a zonal straton characterized by a specific complex of associations of ancient plants, simultaneously existing within a limited territory, established in the framework of the Braun-Blanquet phytosociological system discussed. The version of the scale of plant-associations zones for the Upper Permian sediments of the Pechora basin and the Cis-Urals is proposed.

INTRODUCTION

Numerous publications are devoted to the principles of zonal subdivision and to the term *zone*. The general analysis of the problem may be found in special reports (Krasilov, 1977; Krasilov *et al.*, 1985; International Stratigraphic Guide, 1978; Stepanov and Mesezhnikov, 1979). The idea of recognition of zonal complexes, which might correspond to ancient vegetation changing each other in space and time, is developed as applied to plant megafossils in the framework of the paleoecosystem approach. It might allow to comprehend the zonal scale in the light of real florogenetic and phytocoenogenetic processes.

The most developed version of such an approach in the domestic and, apparently, in international literature is proposed by V.A. Krasilov (Krasilov, 1972, 1977; Krasilov *et al.*, 1985). Krasilov uses the term *coenozone*, which he defines as "a stratigraphic interval, characterized by a stable combination of species in definite quantitative proportions," explaining that "the recurrence of the exact same combination of species and their proportions in successive beds indicates the coenotic equilibrium," whereas the disturbance of the latter "leads to the change of composition and/or quantitative proportions of biofossils, marking boundaries of coenozones" (Krasilov, 1977). The ecological interpretation of coenozone change is based on the reconstruction of primary communities. In the Quaternary deposits, the latter may be reconstructed rather simply using the recent analogues of communities. This is impossible for the more ancient time intervals, and here one must rely only on the burial assemblages. To build a bridge between communities and their subfossil or fossil remains (taphocoena, phytoorictocoena), Krasilov uses the common ecological and phytocoenological term *association*, assigning to it, however, a peculiar meaning. He identifies *association* as a type of taphocoena or phytoorictocoena characterized by a definite composition and proportion of the remains of coenotically connected organisms (from here on, I shall discuss only plants, though Krasilov applies his approach to at least some types of faunal communities – see Krasilov, 1977). These types are represented in concrete sections by recurrent phytoorictocoena. The recognition of types is accomplished by study of the combinations of fossil species in concrete phytoorictocoena, using the method of recurrent groups or cluster analysis. Proceeding from the fact that the composition and quantitative proportions of species in the communities during transformation into fossil or subfossil state undergo significant distortions, such that the preserved quantitative proportions of plant megafossils more or less adequately reflects only "the most general dominance proportions," Krasilov considers that it is possible to be restricted in the analysis by the combinations of dominants only and regards them as fundamental characteristics of his associations. According to Krasilov's concepts (*ibid.*), "the dominants with a low frequency of occurrence belong to the rare local associations, whereas a high abundance with a low indicator of importance (i.e., occurring in many taphocoena, but rarely dominant) may indicate the communities removed from the burial sites." Krasilov used this approach in his study of the Mesozoic flora of the Bureya basin (Krasilov, 1973).

Krasilov's method of recognizing associations and characterizing coenozones provokes a number of principal objections. First, experience in modern

phytocoenology shows that the dominant approach to the classification of phytocoena gives satisfactory results only as applied to a limited number of community types characterized by few stable dominants and a low diversity of ecotopes, e.g., in the case of some placoral boreal forests. Therefore, there are no reasons to use only *a priori* dominants, as Krasilov proposes. As for the fossil material, the problem exists that the ecology of a large number of fossil species, including the dominants of phytocoena, may be characterized, in the best case, by using general terms that are not very definite, such as *hygrophylic*, *mangroves*, and so on. In addition, the correct application of the ecologo-coenotical term *dominant-edificator* requires knowledge not simply of species ecology, but also of its role in the formation of the phytocoenotic environment of the community. Moreover, there are no clear and direct relations between the abundance of a species in the community and its edificatorial significance, which can be used in the indirect determination of the edificatorial significance of an ancient species.

The dominant approach is based theoretically on the so-called "organismistic" model of phytocoenosis. The latter regards communities as real, historically formed integral combinations of populations, interconnected mainly by plant interaction, first of all, between edificator species. This is why the latter are considered as very significant in the classification of communities as their "essential features." According to the organismistic model, the dynamic processes in phytocoena are well-determined and directed toward the formation of stable climax communities. Modern phytocoenology shows that the applicability of the organismistic model is restricted by the above-mentioned oligodominant monoaspect communities with a fairly homogenous ecotope. The so-called "continualistic" model of phytocoenosis is much more universal. In accordance with this model, the phytocoena are regarded as conditionally recognized homogeneous parts of plant cover, where the populations are united by the environmental conditions. The plant cover consists not of separate communities-quasiorganisms, but of a continuum; in other words, it reveals a more or less gradual change of all characteristics in passing from one site to another and nonrigid interrelations of these characteristics (which does not exclude an existence of sharp boundaries in the plant cover!). The changes in separate populations in the processes of phytocoena dynamics are essentially independent of one another, and these processes themselves have a stochastic character, to some degree. It is inferred from the continualistic model that the species-indicators of environmental conditions, determining the formation of corresponding types of communities, have the most important significance for classification. These species need not be highly abundant in the communities. Thus, for the classification of ancient phytocoena, it is preferable to use a continualistic model, which negates the universality of the dominant approach.

Another important objection concerns Krasilov's method in recognizing associations. Basically, it is the practice of the so-called ordination of vegetation. The latter includes species ranking or descriptions of phytocoena along axes reflecting changes in main complex environmental gradients in time (all the so-called methods of direct ordination), or a similarity of the descriptions themselves, determined using the *Sörensen coefficient* or some other method (so-called methods of indirect ordination). Thus, Krasilov's approach, i.e., the method of recurrent groups and the cluster analysis, may be regarded as a variant of indirect ordination. The ordination of vegetation gives on special tables and graphs an objective illustration of species or community distribution in relation to the leading ecological gradients or the variation of the floral diversity of communities in space and time. At the same time, ordination is too descriptive and ideographic a procedure. General concepts covering the main types of phytocoena diversity are required to solve many problems of the theoretical understanding of community structure, dynamics, and ecology. Only the classification of phytocoena may provide these concepts. In this respect, Krasilov's classification term *association*, with respect to the results of ordination, is illogical, meaning only a certain rank in the systematics of phytocoena. It should be noted, however, that many ordination schemes can be reorganized using a special analysis in classification schemes; i.e., they are suitable for classification. It is interesting to note that ordination was proposed by some orthodox supporters of continualism as an alternative to classification, which is not applicable, according to their opinion, to the continuum of plant cover properties, and their diversity may only be "objectively described." Thus, the discrimination principle for associations (dominant) and the method (ordination) are taken by Krasilov from contradicting theoretical sources, continualism and organismism.

Accepting the general idea of characterizing zones by the assemblages of coenotically related plant remains, it is necessary to recognize them by means other than Krasilov's. The approach proposed in this paper is based on the conclusions and results of parasyntaxonomy.

BASIC IDEAS OF PARASYNTAXONOMY

The area of paleogeobotany that involves studying the diversity of ancient plant communities (Ignatiev, 1991, 1992, 1992a) is called parasyntaxonomy. The essence of parasyntaxonomy is the classification of communities, i.e., synsystematics. Its basic ideas may be summarized briefly as follows.

The phytocoenotic diversity of the ancient plant cover came to the present in the form of their fossil remains or phytoorictocoena, preserving in an essentially altered state some of the initial community characteristics such as flora composition, the pattern of plant indicators of species abundance, and so on. The relatively stable combinations of these characteristics

(archetypes), which were typical for ancient communities, are reflected in phytoorictocoena. It permits obtaining a classification of ancient phytocoena on the basis of the study of their fossil remains (Ignatiev, 1992a).

The flora composition of phytocoena reflects their specific nature and connection with initial communities better than other characteristics. The study of modern phytocoena shows that species composition most adequately reflects their syntaxonomic peculiarities caused, first, by environmental factors. Therefore, the floristic principle (Ignatiev, 1992a) should be regarded as a basis for the uniform natural classification of ancient and modern plant communities.

Some fossil species from the composition of phytoorictocoena reflect better than other species the specific features of initial communities, representing ancient species that indicate the paleoenvironmental factors of the formation of a corresponding type of ancient phytocoena. These species (the so-called diagnostic species) are the basis for the recognition of fossil syntaxa (parasyntaxa), i.e., taxa of ancient communities. The problems of recognition of diagnostic species were considered in one of my previous publications (Ignatiev, 1992a).

Because of the continual nature of vegetation, the relation between characteristics of concrete phytocoena is significantly less rigid than it is for objects of traditional systematics – animals and plant species. Hence, the stable combinations of the community characteristics are statistical and may be revealed only from a large number of descriptions. Similarly, the feature space of phytoorictocoena also has a continual character inherited from a continuum of ancient vegetation (the so-called "*phytoorictocoenotic continuum*" – see Ignatiev, 1992a).

In modern phytocoenology, the most developed, widely accepted, and perspectival approach to the classification of vegetation communities is the Braun–Blanquet method. This method is based on a floristic principle and has an intuitive-statistical nature (Mirkin, 1989). The Braun–Blanquet approach technically includes the processing of special phytocoenological tables or suitable computer programs and results in the recognition of nonrank phytocoena types of various volumes and in their following organization into a hierarchic system analogous to the systems of animals and plants (phytosociological system). The Braun–Blanquet approach may be used for the classification of ancient plant communities. The problems of its adaptation to fossil material are regarded in my works (Ignatiev, 1991, 1992, 1992a), where one may find references to the basic literature on this method.

The main ranks of the Braun–Blanquet phytosociological system, in the order of subordination, are a class, an order, an alliance, and an association.

The nomenclature of syntaxa is regulated by an international "Code of phytosociological nomenclature" (Barkman *et al.*, 1988).

The fossil syntaxa (parasyntaxa), which are comparable in composition with modern taxa, are included in the phytosociological system along with modern taxa. The parasyntaxa, which do not correspond to this requirement, may be organized into various formal systems or by some means informally correlated with syntaxa of a natural phytosociological system.

According to the Code, the association is a basic rank of the phytosociological system. It means that the corresponding association must be established on the material of concrete descriptions and typified by such a description before the recognition of syntaxon of any other rank. It is impossible to indicate universal criteria determining the content and volume of association. At the same time, one can state that association is a regional unit with limited area, which reflects mainly horizontal, i.e., geographical changes of vegetation (Mirkin, 1989). From the viewpoint of vegetation dynamics, the association of the Braun–Blanquet system, taken in a narrow regional meaning, corresponds approximately to the so-called demutation-complex, which is determined as "territory occupied by associations belonging to a single stage of ecogenesis (the key association and all associations of its demutation series, if they are present)" (Razumovskii, 1981). It should be explained that "key association" in the terminology of S.M. Razumovskii means the type of communities that are typical for a definite stage of autogenic succession in an undistorted habitat, and "associations of demutation series" are comparatively short-lived types of communities, successive sequences of which regenerate the basic association in the places of distortion of its biotope.

PLANT-ASSOCIATIONS ZONES AND PALEOGEOBOTANIC INTERPRETATION OF PALEOSUCCESSIONS

I define a plant-associations zone as a zonal straton characterized by a definite complex of co-existing associations of ancient plants within a limited territory. These associations are recognized in the framework of the Braun–Blanquet phytosociological system. The names of plant-associations zones consist of one or two names of assemblages characterizing the corresponding zone, for example, the *Cordaito candalepensis–Ruflorietum synensis* association zone (see below).

This suggests that plant-associations zones are regional units. The paleogeobotanic and paleofloristic content of the plant-associations zone is similar to A.I. Tolmachev's "concrete flora." According to his ideas (Tolmachev, 1986), "theoretically, the concrete flora must meet the following requirements: the combination of the composing species is distributed over the entire region occupied by the flora, forming various groups and occupying separate parts of the area according to the local peculiarities of every site; the same species combinations should correspond within the region to sites of similar conditions; in other words, each concrete association of the region should have a stable floral

composition; moreover, this regularity should be repeated in all the occurring associations of the region. Thus, the floral differences between separate parts of the region will directly reflect the peculiarities of a given site, whereas in the regions florally different in a strict sense, we can meet various species combinations except for the total coincidence of local conditions." Thus, the concrete flora is characterized in the area of habitat by a uniform composition and a similar complex of associations that are in definite successional relations between one another. From a dynamic point of view, it is a self-supporting and dynamically stable system, a *homeostate* (Razumovskii, 1981). All variations of floral composition in the region of the concrete floral habitat are caused by local peculiarities of the biotope, not by macroclimate fluctuations.

I must emphasize that it would be unrealistic to identify syntaxonomic characteristics of plant-associations zones with ancient concrete floras. The fossil associations are not entirely comparable in composition with the modern ones because of defects in the fossil material. Similarly, the combination of these associations in the composition of the corresponding ancient concrete flora may not be complete. Hence, the ancient concrete floras are generally a subject of more complex reconstructions.

Associations of fossil species established in the framework of the Braun–Blanquet approach are the most detailed natural units, which can be outlined in the paleosuccession at the coenotical level. They are the most detailed because the concrete phytoorictocoena used in their definition are the smallest units of the paleosuccession. They are natural as reflectors of the syntaxonomical structure of the continuum of the ancient vegetation.

Similarly, the series of simultaneously existing and, perhaps, successively related associations of fossil plants is the most detailed natural subdivision of paleosuccession at the floral level, being comparable with Tolmachev's concrete floras (see above).

Thus, the plant-associations zones are the most detailed natural units of the stratigraphic subdivision of continental plant-bearing deposits.

Spatially, the plant-associations zones can be mapped as subdivisions, with boundaries corresponding to the limits of geological bodies formed under the definite environment of sedimentation within the area of corresponding ancient concrete flora.

The succession of plant-associations zones in the general case should be regarded as a result of macroclimate changes or other reasons, which are able to produce transformations of the same scale, because the coenotical differences in the distribution area of any concrete flora are caused by local environmental conditions (see above). The problem of factors causing the replacement of zones is a subject of special study. Moreover, any changes taking place at the coenotical level are not obviously related to macroclimate changes only and may be caused by an autochthonous species evolution, penetration of alien species into communities, or by a number of other coenotical processes. They are also subjects of independent study.

It is necessary to mention again Krasilov's concept (Krasilov, 1972, 1977; Krasilov *et al.*, 1985) regarding the problems of the paleogeobotanic interpretation of the scale of plant-associations zones. According to Krasilov's ideas, the so-called regional *catena*, means the regional distribution of soil and vegetation belts responding to changes in leading environmental factors by a displacement of their elements. The catena is at the base of a regional coenozone system (in the abovementioned understanding). The reconstruction of catena may be illustrated schematically in Krasilov's words: "Because the material is transported down the slope, the allochthonous elements (b) in the catena, consisting of three links, "a," "b," and "c," will be found among the remains of "a;" the allochthonous elements "c," among remains of "b" and to a lesser degree among those of "a;" whereas the occurrence of elements "a" among "b" or "c" is unlikely. We can obtain the fullest impression about the upper belts in these cases: (1) when marine or limnic water floods depressions with vegetation; (2) when coastal brushwoods act as a filter and prevent the migration of remains through water, and the plants organs, are transported primarily through the air from the uplifts; (3) when the link migration takes place, shifting the upper belt toward the burial place, which is reflected immediately on the frequency of species distribution" (Krasilov *et al.*, 1985).

"The spatial relationships between belts are stable for long distances. Each regional catena has its own peculiarities, reflecting the local conditions of belt differentiation. Moreover, catenas of various provinces and various ages often have common elements, allowing their similar links to be revealed and a system of vicarious catenas to be defined... The system of vicarious catenas reflects both biogeographical (number of links and their position in the catena) and age (change of communities in vertical columns) relations. One can discern a migrational change of species in the chronoclines from an autochthonous evolution only using such systems... The reorganization of catena is one of the indicators of the distortion of coenotical equilibrium, determining the ecostratigraphical boundary. The changes in the slope relief may induce the fallout of some biotopes... or the telescoping of belts... The basic factor controlling the belt distribution... of terrestrial communities is temperature. Hence, a climate change synchronizes the reorganization of various catenas. A catena may be regarded as a stable polyclimax, and its reorganization, as a change of climaxes or a cliseria" (Krasilov, 1977).

Krasilov's catenary model leaves open some important questions. First, to identify in phytoorictocoena such types of "zonation" different as the altitudinal zonation (in geobotanic meaning) of high mountains, the zonation of placore forests, and the vegetation "belts" of the flood-plain forest observed in passing from the forebank to the backlevee, it is not enough to

have only indications of the regional scale. For example, in the alluvial environments the phytoorictocoena predominantly reflect vegetation growing very close to reservoirs and waterstreams. From a geographic point of view, this vegetation is extrazonal to some degree because of the specific habitat. If one can use the term "zonation" in such cases, it would be applicable only to the ecological series of local communities.

The identification of the catena link with the association also seems to be groundless. There is usually a large number of essentially syntaxonomically different types of communities of a regional scale within one belt that belongs either to altitudinal or to vegetation zones. The belt model itself is a particular case of the more universal mosaic distribution of communities.

The firm relations between the phytocoena and facies or between the allochthonous character of species and the affiliation of corresponding plants to the "higher" links of the catena supposed implicitly by Krasilov cannot be accepted without serious doubts. The definite type of phytoorictocoena is connected with facies only statistically, and the degree to which they are allochthonous is highly dependent on the character of the remains. Each type of ancient community is represented in fossil state simultaneously by several types of phytoorictocoena, differing in flora composition, in proportions of species abundance, in degree of allochthony, and in other indicators, just as a single species of ancient plant is represented by the remains of its dispersed organs of varying degrees of preservation. It does not follow from Krasilov's above-mentioned example that elements "c" belong to plants of higher link of catena than "a" and "b," even if the suggested relations of autochthony-allochthony remain valid. The corresponding phytocoena may belong, for example, to a community that was in "altitudinal" aspect at the same level with "a" and "b" but had a tendency to form allochthonous phytoorictocoena and to add to the allochthonous elements other types of phytoorictocoena because of its biological peculiarities and position with respect to a reservoir or waterstream.

The reconstruction of catenas is a particular case of the so-called paleogeobotanic ordination, i.e., it is the reconstruction of an ecological series of ancient communities in relation to the leading gradients of paleoenvironments (Ignatiev, 1991). In the case of Krasilov's catenas, we are dealing with ordination along the altitudinal gradient.

The understanding of the catena as a stable natural formation responding to changes of macroclimate by the displacement of links is not valid enough in my opinion. To support his ideas, Krasilov refers to "the law of relative stability of habitat and biotope changes," formulated by H. Walter. Krasilov (1977) writes, "Walter (1968) proposed a rule of biotope changes, according to which the biogeocoenotical system reacts to changes of conditions by the displacement of links." In fact, Walter's law affirms that "in the case of a climate change in the area of certain species, the replacement of biotopes by this species takes place in such a way as to compensate for the climate change; thus, the conditions of habitat in various biotopes remain more or less similar" (Walter, 1968). It means, for example, that the species tends to occupy more and more humid biotopes under an increasingly arid climate. Thus, there is nothing about biogeocoenotical systems and link displacement in Walter's law, and only a definite tendency of species ecology is under discussion. In passing to the community level, one can hardly conclude from this tendency that all of the community species migrate uniformly toward the environmental conditions that compensate for macroclimate changes. The degree of integration of plant communities is not high enough, and species ecology is too "individual" to account for only "link displacement" without rather deep changes inside communities under the macroclimate fluctuations. In fact, one can imagine partly what is taking place by regarding the situation on wide placores, where a clear succession of vegetation zones is observed. The changes in species ecology noted by Walter occur here as various extrazonal phenomena. These have long been known to botanist-geographers, and the respective generalization known as V.V. Alekhin's "antecedence rule" was formulated earlier and independently of Walter's law. This rule states that "placoral species, or a placoral phytocoenosis, is antecedent from the south or from the north of the respective habitat environments" (Alekhin, 1936; cited from Alekhin, 1989, p. 38). Moreover, as Alekhin remarks (*ibid.*), "the extrazonal phenomena are more typical and occur more frequently, the closer they are to their own zone; the extrazonal echoes in more distal subzones become rarer, being manifested not so typically, until finally, they completely fade" (emphasis mine). It should be noted that extrazonal phenomena are not connected for certain with macroclimate changes, but they may be caused, for example, by the presence of a habitat system, enabling them to compensate for differences in the macroclimate. The penetration of forests inside the steppe zone along river valleys is a well-known example. However, the communities do not prograde here in an unchanged form, though Alekhin's remark above remains completely valid.

The discussion above permits the supposition that the migration of zonal types of communities may to a small degree be "the first reaction" of already-formed succession systems to the macroclimate changes. However, the somewhat deep reorganization of communities in the following stages takes place during strong and continuous unidirectional climate changes, as is evident from "the damping" and the increasing "atypical" character of extrazonal echoes in moving away from the boundaries of maternal zone.

The parasyntaxonomy of ancient phytocoena is not related to any model of the plant cover structure like those of catenas, vegetation zones, or other categories. In the worst case, when we cannot satisfactorily interpret a paleosuccession in the paleoecological aspect, the parasyntaxonomical analysis gives a paleogeobotanically clear, uniform, and explicit subdivision of

the succession into complexes convenient for purely formal stratigraphic correlations. These correlations are based, in any scale of correlation, on the actually observed similarity of phytoorictocoena reflected in the syntaxa of various ranks of the phytosociological system. The strict geobotanic nomenclature of coenotically related complexes of plant remains is the other advantage of the approach.

On the other hand, understanding the nature of phytostratigraphic boundaries in a methodological aspect is possible only through the projection of the ideal structural and dynamic models of modern vegetation upon the historical evidence of the ancient plant cover (Ignatiev, 1992a). The reliability of such projections is estimated by the comparison of ancient and modern plant communities in terms of the phytosociological system. Thus, the parasyntaxonomy is a necessary methodological base for ecostratigraphy, with respect to the ancient plant cover.

SCALE OF THE UPPER PERMIAN PLANT-ASSOCIATIONS ZONES OF THE PECHORA BASIN AND THE CIS-URALS

I conducted a parasyntaxonomical study (Ignatiev, 1991) of the phytoorictocoena from the Upper Permian of the Pechora basin and the Cis-Urals with the material of basic sections on the Adz'va and the Bolshaya Syna Rivers. The obtained results allowed developing a version of the plant-associations zones scale shown in Fig. 1. It is possible to give here only the brief characteristics of this scale because of the limited scope of this paper, in order to illustrate a proposed approach to the recognition of zones, using a concrete example. It is regarded more comprehensively in another paper that I am preparing.

Three successive plant-associations zones are established: *Ruflorietum obovatae*, *Cordaito brevis–Ruflorietum sylovaensis*, and *Cordaito candalepensis–Ruflorietum synensis*. They cover the larger part of the Pechora deposits' volume, excluding their uppermost and lowermost parts. There is not enough data at our disposal on these intervals of the section to define associations of fossil plants. At the same time, the peculiarity of their phytoorictocoena allows us to suppose that they will be further classified as separate zones.

Parasyntaxonomical analysis allows recognizing three main types of the phytoorictocoena in the paleosuccession of the Pechora Basin, corresponding to the three co-existing types of ancient communities of the Pechora time. These communities are attributed to the classes *Cordaito–Ruflorietea* Ignatiev, *Phylladodermetea* Ignatiev, and *Peltaspermo–Rhachiphylletea* Ignatiev (Ignatiev, 1991).

The communities of the *Cordaito–Ruflorietea* and the *Phylladodermetea* classes are two main types of the flood-plain forests of the Pechora time. The various species of cordaitean plants had formed a canopy and a part of the base in the cordaitean associations, whereas ferns produce the grass cover. Apparently, these communities grew predominantly on higher areas of the levee. In contrast, the phylladodermian phytocoena occupied swampy parts of the levee, where the intensive peat accumulation took place over rather wide areas. The abundant leaf fall of *Phylladoderma* Zalessky provided the main material for the latter. These leaves, covering the soil in a thick layer in the phylladodermian phytocoena (phylladoderms were, apparently, shrub-wood trees or shrubs), prevented the development of other species, including cordaitean plants, so that these communities were, perhaps, almost pure thickets of one or several species of phylladoderms.

Phytocoena of the *Peltaspermo–Rhachiphylletea* class represented the locally distributed thickets of one or several species of the "pechorian" callipterids, occurring in the forebank. Apparently, the growth form of these plants was similar to the modern large boreal ferns.

The change of cordaitean associations is used as the main characteristic of the established zones, which is reflected in their names. The species systematics of phylladoderms remains thus far unsatisfactory. It did not allow subdividing into units the phylladodermian "branch" of the paleosuccession, which is defined conditionally as the uniform *Phylladodermetum arberi* Ignatiev association. At the same time, one can suppose that there are at least three members within it according to available data (Ignatiev, 1991). In the future, such a subdivision will allow obtaining more precise characteristics of established zones.

The "cordaitean" base of the proposed scale of plant-associations zones has the distinction of being the phytocoena of the dominating, or of one of the dominating types, not only for the Upper Permian, but for the entire Permian continental plant-bearing deposits of the Pechora basin and the Cis-Urals (see, for example, Uglenosnaya Formatsiya..., 1990). The change of cordaitean associations was caused, apparently, by macroclimate changes leading to their destabilization and changes in species composition. The role of the autochthonous evolution of species was relatively minor. In particular, the ruflorians of the Vorcuta type are connected, perhaps, with the ruflorians of the *R. sylovaensis* (Neuburg) Ignatiev group, and the ruflorians of the "*obovata*" type, with ruflorians of the *R. synensis* (Zalessky) Meyen group. The cordaitean communities, which earlier were the main coal creators, were replaced in swampy parts of river valleys by phylladoderms at the end of the Seidian. Perhaps this was caused by evolutionary changes in the reproductive sphere of the phylladoderms, i.e., by the formation of the closed seed-bearing capsules of the *Cardiolepis* Neuburg type instead of open peltoids. These capsules, having fleshy envelopes and air bladders providing buoyancy, became the main diaspores of phylladoderms instead of separate seeds without accessories for distribution through water or air. The new advantages allowed competing successfully with cordaites in the colonization of places of levees constantly distorted by hydrological processes.

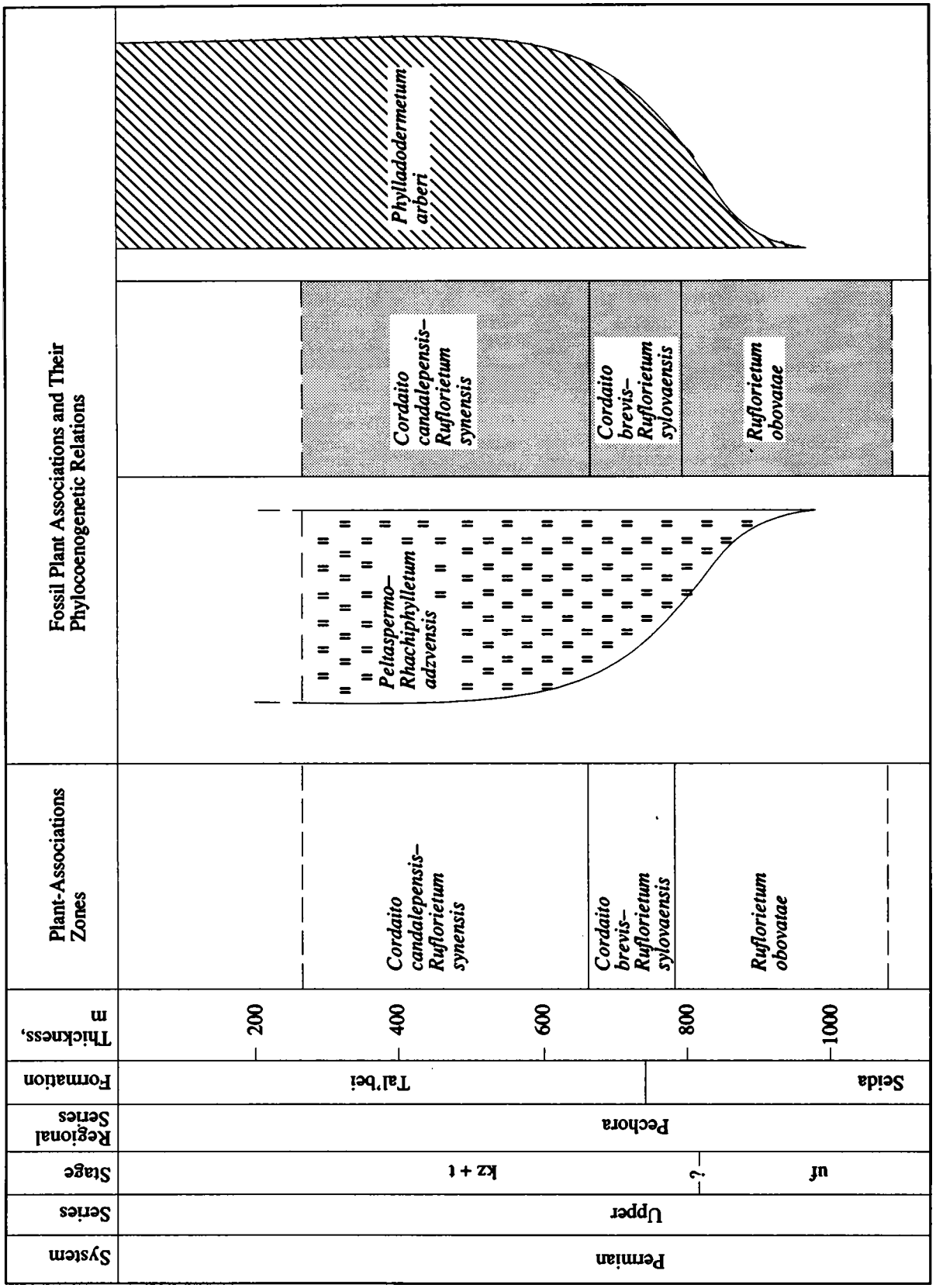

Fig. 1. *Scheme of zonal subdivision of the Upper Permian deposits in the Pechora basin and the Cis-Urals on the basis of fossil plant associations.* The thicknesses of formations and the boundaries of plant-associations zones are shown on the key section of the Adz'va River.

The associations of the *Peltaspermo–Rhachiphylletea* class are the most unfavorable for stratigraphy, though the boundary of the Vorkuta and the Pechora beds is difined traditionally by the first appearance of callipterids. Callipterids had penetrated, apparently, the territory of the Pechora basin and the Cis-Urals through the river valleys from an area corresponding to the modern Middle Cis-Urals. This process took place during a significant part of the Vorkuta time, which is indicated by separate finds of callipterids in the deposits of the Inta Formation and even in the Rudnitskaya Subformation of the Vorkuta Group. However, these plants did not play any significant role in the plant cover during the Pechora time, forming small local clumps of one or several species, or occurring as an admixture in other types of phytocoena. To a large extent, it is connected with the organization of the reproductive sphere of these plants, which were typical barochores. Their relatively rare and sometimes large seeds without special accessories for wide distribution were located on the open peltoids and, having fallen because of gravitation (barochoria), germinated frequently next to the maternal plants. The low frequency of occurrence inherited from the local distribution of maternal communities makes the callipterid phytoorictocoena unsuitable for the definition of stratigraphic boundaries. It is incomparably more convenient to fix events, producing the stratigraphic boundaries by changes in the dominating types of ancient vegetation. However, it does not exclude the possibility of using callipterid associations for the characteristics of plant-associations zones.

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Evolution of Planktonic Foraminifers of the Warm-Water Pacific in the Paleogene

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Abstract – The analysis of distribution and changes in the taxonomic composition of zonal complexes of planktonic foraminifers in Cenozoic sections penetrated by deep sea drilling holes in the tropical and subtropical areas, reveals periods of increased rates of the evolution of this fauna throughout the Paleogene. It promoted a renewal of zonal complexes up the section at the expense of increasing rates of extinction and origination of species. The greatest bursts of evolutionary activity occurred at the Paleocene-Eocene boundary, and in the late Eocene and the earliest Oligocene. The late Oligocene was marked by an increase in the origination of new species. A period of activization of evolutionary changes in planktonic foraminifers was accompanied by a structural reorganization of their associations and by changes in ecological types, coinciding in time with major tectonic, oceanologic, and climatic events.

In ocean history, the Paleogene was a time of great oceanologic and climatic reorganizations. This is apparent in the structure and composition of the sedimentary cover and in changes in various planktonic and benthic species associations. Micropaleontological and isotopic investigations in oceans indicate that tectonic reorganization in the South Ocean in the Paleogene resulted in changes in the character of bottom and surface circulation as well as in its forcing mechanism. Haline circulation was characteristic of the oceans in the Cretaceous–early Paleogene periods, when dense and saline water sank in the low latitudes and spread out toward the poles. As a result, the ocean was evenly warmed and developed a sluggish circulation along with a weakly expressed latitudinal zonality and low temperature gradients.

The successive northward motion of the Australian lithospheric block, which began at the Paleocene-Eocene boundary (Weissel and Hayes, 1972), together with the Drake Passage opening in the very late Oligocene (Barker and Burrell, 1977), which promoted the onset of the Circum-Pacific Current and thermal isolation of the Antarctic, resulted in the transformation of a haline circulation into a thermohaline one by the end of the Paleogene. The well expressed latitudinal and vertical thermal gradients served as the main dynamic mechanism of the newly formed circulation. The transformation of oceanic circulation was accompanied and simultaneously controlled by a global cooling which began at the late-early to early-middle Eocene and lasted through the Cenozoic accompanied by a sharp fall and a relative rise in bottom and surface water temperatures during certain periods.

The cooling trend through most of the Cenozoic was established by isotopic studies in many regions of the World Ocean (Douglas and Savin, 1973, 1975; Shackleton and Kennett, 1977; Buchardt, 1978; Boersma and Shackleton, 1977; Vergnaud-Grazzini *et al.*, 1978; Douglas and Woodruff, 1981; Oberhänsli *et al.*, 1984; Shackleton *et al.*, 1984; Miller *et al.*, 1987, and others). It is well-expressed in high latitudes, where temperature fluctuations displayed greater contrast, as compared to those in the equatorial-tropical area. According to the data of N. Shackleton and J. Kennett, (Shackleton and Kennett, 1975), the highest surface water temperatures occurred in the late Paleocene–early Eocene in the Australia–New Zealand region of the Pacific. These temperatures ranged from 15 to 20°C lowering by the end of the early Eocene up to 12 - 14°C. In the middle-late Eocene, they fell gradually to 10°C by the end of the Eocene. The surface water temperature sharply dropped to between 6 and 7°C at the Eocene–Oligocene boundary, remaining near this value through the Oligocene. Only during the middle Oligocene did it rise slightly to 8°C.

The impact of climate fluctuations and, correspondingly, of surface water temperature changes on the composition and diversity of planktonic foraminifers is well known at present. This manifests itself more distinctly in high latitudes, where climatic fluctuations are characterized by a high amplitude, and planktonic foraminifers dwelling in near marginal conditions respond readily to changes in temperature. In warm areas of the ocean, temperature fluctuations show less contrast, and, in general, affect the planktonic foraminifer diversity to a much lesser degree. Nevertheless, their composition changes signficantly in accord with climatic fluctuations. G. Keller (1983a, 1983b) argues that during pronounced cooling periods in tropical areas of the Atlantic, Indian, and Pacific oceans, at the Eocene–Oli-

gocene boundary in particular, the role of the so-called intermediate and still cooler deep water species in the planktonic foraminifer association increased significantly, leading to a decrease in the numbers of surface thermophilic species.

The influence of paleoceanological and paleoclimatic events on the planktonic foraminifer fauna was not restricted to changes in their composition, abundance, or species diversity, which occur in response to temperature fluctuations of surface water. These events affected also their evolutionary activity. Changes in evolutionary activity are well identified in the warm-water oceanic realm. In high latitudes, the appearance and disappearance of planktonic foraminifer species in sedimentary sequences are a result of environmental changes rather than evolution.

Recently, interest was rekindled in the evolutionary changes of planktonic foraminifers in the Paleogene. R.M. Corfield (Corfield, 1987; Corfield and Shackleton, 1988), analyzed the rate of evolutionary changes in planktonic foraminifers at the Walvis Ridge (Site 527) and Shatsky Rise (Site 577) in the Paleocene–early Eocene. Using a precise correlation between the datum levels of the appearance and extinction of the foraminifer species to the paleomagnetic and nannofossil scales, Corfield inferred that the highest rate of evolutionary activity of planktonic foraminifers falls within the 62 - 64 and 56 - 59 Ma intervals, i.e. approximately coincides the early-late Paleocene and Paleocene–Eocene boundaries.

Unfortunately, the dating of evolutionary events is far from being perfect, when one takes into consideration the difficulties in pinpointing the appearance and extinction of species, and interpreting the magnetic inversions in the Paleogene sections, especially if there are hiatuses. Moreover, Paleogene sections with both reliable paleomagnetic dating and good paleontological characteristics are still deficient at present. In addition, the dating of paleomagnetic events change constantly. A good example of this is found in the new scale developed by S.C. Cande and D.V. Kent (Cande and Kent, 1992) which is different from that of W.A. Berggren *et al.* (1985). This is also seen in the mentioned publications in which Corfield, using the same sections, cited several different dates of the same evolutionary events. For this reason, when conducting these types of investigations, it is probably better to deal with the zonal biostratigraphic rather than with the geochronological scale, and use the latter only as a reference. Application of the zonal scale allows us to use a larger number of sections, and thus, to obtain the mean and unbiased data.

This approach was chosen when studying Paleogene evolutionary changes in the planktonic foraminifers in the warm-water Pacific.

An earlier analysis of foraminifer composition and distribution in the Pacific Paleogene sediments that had been penetrated by deep sea drilling (Krasheninnikov, 1982; Krasheninnikov *et al.*, 1988) showed that they

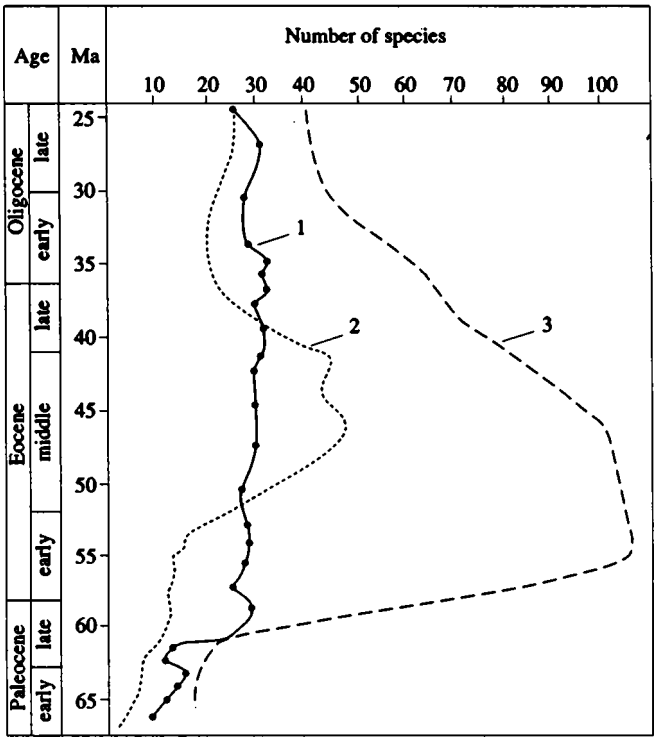

Fig. 1. *Species diversity of the Paleogene planktonic foraminifers.*
1 – in the present publication; 2 – Toumarkine, 1983; 3 – of the calcareous nannofossil (Haq, 1973).

displayed a high species diversity and a rapid evolutionary renewal of associations. This permits us to make a detailed subdivision of carbonate sequences, distinguishing the zones of a standard scale.

More than 200 species comprise the Pacific Paleogene foraminifer fauna. Moreover, the species diversity of the zonal complexes up the section undergoes no dramatic changes. The curve of variations in species diversity of zonal complexes, compiled for warm water areas of the Pacific (Fig. 1), shows that after the total extinction at the Mesozoic–Cenozoic boundary, planktonic foraminifers reappear in the Paleocene basal layers (the *Globigerina eugubina* Zone) and comprise nine species. Throughout the early Paleocene, the species diversity increases twofold, and in the first half of the late Paleocene (the *Globorotalia angulata* and *Globorotalia pusilla* zones) it increases again to 11 or 12 species. The very late Paleocene (the *Globorotalia velascoensis* Zone) is marked by a steep increase in foraminifer diversity (to 29 species). In the Eocene basal layers (the *Globorotalia subbotinae* Zone), it drops slightly again to 25 species, and then increases gradually to 33 species at the Eocene–Oligocene boundary. In the Oligocene, it usually ranges from 26 - 28 species, increasing to 31 species in the second half of the Oligocene (the *Globigerina ciperoensis* Zone).

The curve of the Paleogene planktonic foraminifer diversity, for the tropical-subtropical Pacific, correlates

well with a similar curve compiled earlier by M. Toumarkine (Toumarkine, 1983) for the entire warm-water area. However, according to data presented in this study, a sudden increase in species diversity occurred in the Pacific much earlier, during the very late Paleocene, i.e., almost simultaneously with an abrupt increase in carbonate nannofossil diversity (Haq *et al.*, 1977).

The curve demonstrating changes in the evolutionary activity of planktonic foraminifers through the Paleogene displays a different pattern. The analysis of species origination and extinction through time indicates that in the Paleogene, the periods of activization of these processes alternate with those of a more stable behavior of the foraminiferal fauna. Based on this inference, several evolutionary stages may be distinguished (Fig. 2):

(1) In the early Paleocene–the first half of the late Paleocene (the interval of the *Globigerina eugubina–Globorotalia pusilla* zones), the renewal of zonal complexes caused by the origination and extinction of species demonstrates a stable character. This stage represents the start of evolution and the formation of the Cenozoic foraminifer fauna after its total extinction at the Cretaceous–Paleogene boundary, and is characterized by a dominance of species origination over extinction. Only in the earliest late Paleocene, does the number of extinct species become greater than that of those newly appearing, a process lending to a decrease in species diversity.

(2) The situation changed dramatically in the second half of the late Paleocene and in the earliest Eocene (the interval of the *Globorotalia pseudomenardii–Globorotalia subbotinae* zones), when the rates of species origination and extinction experienced significant variations. Moreover, while the former abruptly increased in the late Paleocene (a total of 29 new species appeared), the latter remained at the same level as it was in the preceding stage (6 - 8 species per zone). Accordingly, the species diversity increased sharply to reach 29 species per complex in the very late Paleocene.

The Paleocene–Eocene boundary is marked by the extinction of planktonic foraminifers, the most pronounced extinction during the Paleogene. Twenty one species from the Paleocene association do not appear in the basal *Globorotalia subbotinae* Zone of the Eocene. At the same time, the number of new species appearing here was equal to that in the latest Paleocene, reaching 15 species.

(3) During most of the early and the entire middle Eocene (the interval of the *Globorotalia aragonensis* through *Truncorotaloides rohri* zones), the evolutionary activity of planktonic foraminifers remained relatively stable, though the rates of origination and extinction varied here as well (from 5 to 9 and from 2 to 10 species, respectively). These fluctuations were synchronous, but in general, the foraminifer fauna was renovated with a slight prevalence of appearances over extinctions, so that the species diversity of zonal complexes grew, insignificantly though steadily, through the early-middle Eocene, from 25 species in the *Globorotalia subbotinae* Zone to 31 species in *Truncorotaloides rohri* Zone.

(4) The Late Eocene stage of foraminifer evolution was marked by a new outburst of evolutionary activity although not as well manifested as in the very late Paleocene–early Eocene. Moreover, during the late Eocene, evolutionary activity experienced rather significant changes. So, if at the beginning of this stage (the *Globigerapsis semiinvoluta* Zone), the number of appearing and extinct species of planktonic foraminifers was high (15 and 5 species, respectively), then in the mid-late Eocene (the *Globorotalia cocoaensis* Zone) their numbers decrease to a minimum (1 and 3 species, respectively). At the end of the stage (the *Globorotalia centralis–Globigerina gortanii* Zone), nine species became extinct and the same number appeared. The total species diversity changed insignificantly in the late Eocene.

The increased rate of foraminifer extinction was also registered in the late Eocene in the tropical areas of the Atlantic, Indian, and Pacific oceans (Corliss *et al.*, 1984).

(5) During the greater part of the Oligocene, the evolutionary activity of foraminifers fell again. Two to five species usually appear in zonal complexes of the Oligocene. However, in the late Oligocene (the *Globigerina ciperoensis* Zone), 11 species appeared. Six to seven species, and no more, usually die out per zone. In the Oligocene, the total diversity of foraminifers decreased as well, averaging 26 - 28 species.

Thus, two periods of increased rates of foraminifer fauna evolution are registered in the Paleogene. The first period encompasses the latest Paleocene–early Eocene, and the second coincides with the late Eocene. A slight activization in foraminifer evolution was recorded in the latest Oligocene as well.

These periods, characterized by acceleration of renovation of planktonic foraminifer composition because of the extinction of some species and the origination of the new ones, are also marked by major taxonomical reorganization of their complexes. Thus, in the very late Paleocene, the foraminifer association, in which primitive globigerinids, hiloguembelinids, and later acarininids dominated, was replaced with an association in which, together with acarininids, a new group of planktonic foraminifers prevailed (i.e., keeled and conical globorotaliids, which appeared here for the first time).

Nannofossil associations experienced similar qualitative changes in the late Paleocene. At that time, various forms with massive elements appeared and spread widely (large fasciculites, heliolites, discoasters) (Shcherbinina, 1992).

The late Eocene is characterized by changes in the foraminifer association pattern. By that time, some large groups such as acarininids, truncorotalloids and keeled-conical globorotaliids became extinct, whereas relatively cooler forms of globigerinids and globorotaliids (the *G. centralis–G. cerroazulensis* group)

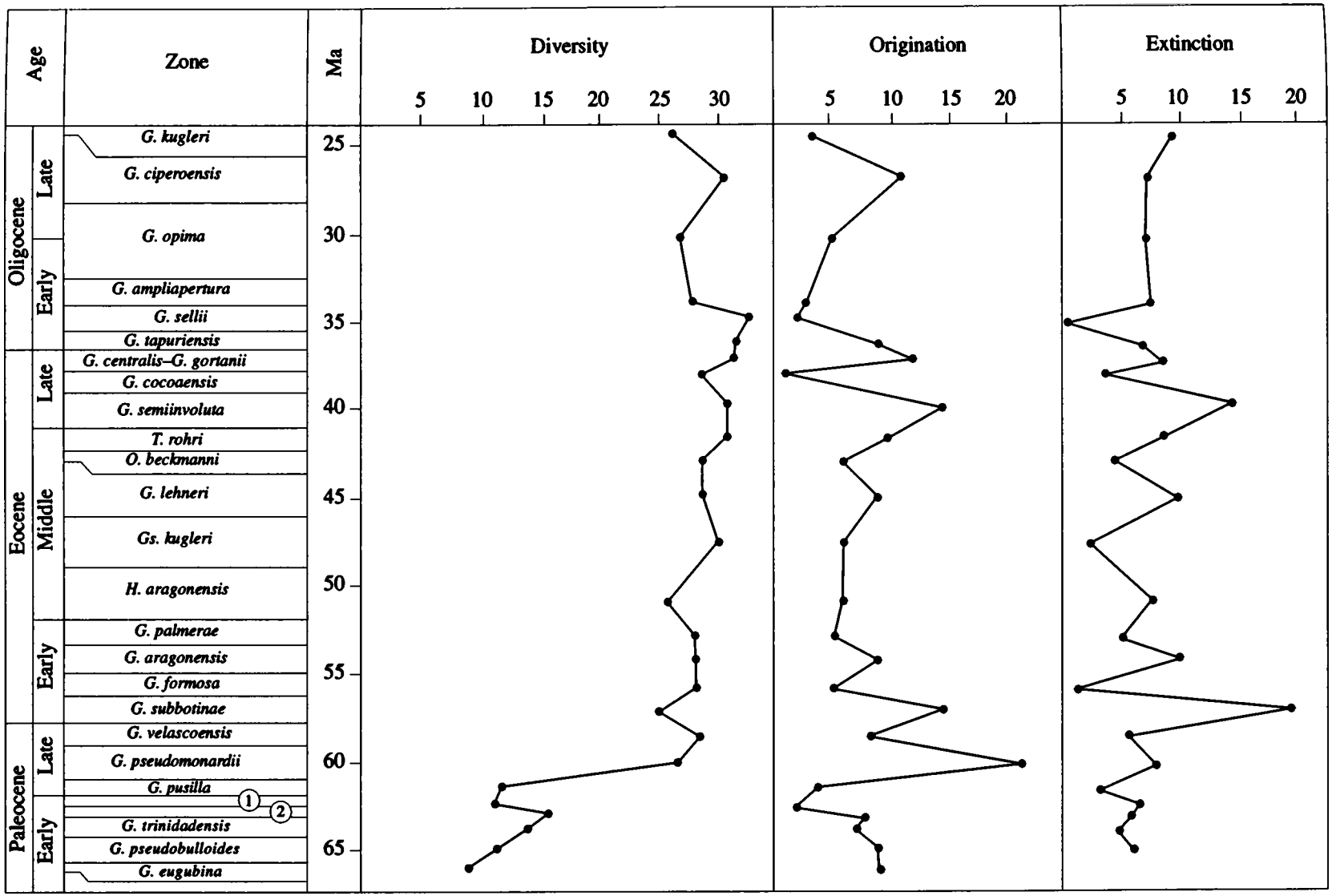

Fig. 2. *Correlation of changes in diversity, origination and extinctions of planktonic foraminifers in the Pacific with the Paleogene zonal scale.*
1 – the Globorotalia angulata Zone and 2 – the Acarinina uncinata Zone. The absolute time scale after Berggren *et al.*, 1985.

assumed a significant role. By the Eocene–Oligocene boundary, representatives of some warm-water genera *Hantkenina*, *Globigerapsis*, *Globigerinatheca*, also became extinct, and *Globigerina* and *Turborotalia* cosmopolitan species, which are the principal constituents of the planktonic foraminifer association in the Oligocene, appeared.

In the late Oligocene, most critical changes in the foraminiferal composition occurred at the *Globorotalia opima–Globigerina ciperoensis* zone's boundary. By this time, the cold water species *Globigerina ampliapertura*, *G. linaperta*, *G. angiporoides*, *G. galavisi*, and *G. ouchitaensis*, and many species of *Turborotalia* (*Globorotalia* (*Turborotalia*) *opima*, *G.* (*T.*) *munda*, *G.* (*T.*) *gemma*) became extinct or lost their dominant role. Simultaneously, many new species (*Globigerina ciperoensis*, *Globorotalia pseudokugleri*, *G. siakensis*, *G. semivera*, *G. mendacis*, *Globoquadrina venezuelana*, *G. praedehiscens*, *Catapsydrax prestainforti*, *C. dissimilis*) appeared in the *Globigerina ciperoensis* Zone. These species are relatively more thermophilic as compared to the undoubtedly cooler species of the early Oligocene association, and later form the main body of the Miocene foraminiferal fauna.

Such evolutionary changes in planktonic foraminifer associations can apparently be explained by dramatic paleoceanological and paleoclimatic events at those boundaries, as well as by the different effect of these events at high and low latitudes of the ocean (Fig. 3).

A global warming from the latest Paleocene to the first half of the early Eocene (the Eocene optimum) was established long ago by isotopic and paleontological studies conducted in many regions of the Earth. This warming occurred after a drop in temperature at the Cretaceous–Paleogene boundary and its gradual rise throughout the early and earliest late Paleocene. A dramatic rise in surface and bottom water temperatures at this time is confirmed by isotopic studies in different regions of the World Ocean (Shackleton and Kennett, 1975; Boersma and Shackleton, 1977; Vergnaud-Grazzini *et al.*, 1978; Letolle *et al.*, 1979; Vergnaud-Grazzini and Rabussier-Lointier, 1980; Oberhänsli *et al.*, 1984; and others). The warming coinciding in time with the sea-level rise, i.e., the Iprian transgression (Vail and Hardenbol, 1979), resulted in the expansion of the ocean warm area. This is proved, in particular, by the immigration of thermophilic associations of planktonic foraminifers and nannoplankton into high latitudes in the late Paleocene–early Eocene (Haq *et al.*, 1977). Thus, the potential area for planktonic foraminifer settling was extended. This led to a considerable increase in the origination of new species and even new ecological groups, as well as in an abrupt rise in species diversity in the late Paleocene.

It is important to note that the rate of extinction in every zone of the late Paleocene was low. The highest rate of extinction corresponds with the earliest Eocene (the boundary between the *Globorotalia velascoensis* and *Globorotalia subbotinae* zones). Considering that three-fourths of the late Paleocene species became extinct at the Paleocene–Eocene boundary, it is evident that the extinction was a result of a primary oceanological reorganization.

Recently, much data were obtained indicating that the Paleocene–Eocene boundary is very important in the Cenozoic history of the ocean. This boundary was marked by global geological and paleoceanological events that affected the evolution of oceanic biota, including foraminifers. Very near this boundary, a major tectonic reorganization occurred, which was accompanied by reorganization of spreading centers and transform faults in the Pacific (Rea and Dixon, 1983), by the opening of the Norway–Greenland basin and the initiation of water exchange between the Arctic and Atlantic oceans (Berggren and Hollister, 1977; Roberts *et al.*, 1984), and by rifting between Australia and Antarctica (Weissel and Hayes, 1972; Scotese *et al.*, 1988). A sudden increase in ^{18}O and ^{13}C isotope content in planktonic foraminifer shells and in carbonate sediments in general, which are found in many regions of the World Ocean, is confined to the first half of the early Eocene (Shackleton and Kennett, 1975; Shackleton and Hall, 1984; Oberhänsli and Hsü, 1986; Shackleton, 1986).

The early Eocene was also marked by a sharp decline in the supply of eolian material to the central parts of oceans and, accordingly, by a decrease in its grain size (Rea *et al.*, 1985; Rea *et al.*, 1990; Rea, 1989; Hovan and Rea, 1992), which is related to the weakening of atmospheric and oceanic circulation. Though the data are inconsistent with the generally accepted idea concerning intensification of circulation during cooling periods, they nevertheless indicate a primary oceanological reorganization at that time.

The evolutionary activity of planktonic foraminifers in the latest Paleocene–early Eocene, consisting of rapid taxonomical renovation because of mass origination (including new ecological types), followed by the extinction of species, was caused by a sequence of these paleoceanological and paleoclimatic events. These events, as was revealed recently, affected the planktonic foraminifer association dwelling in the surface water, as well as the benthic fauna. So, the composition of benthic foraminifers, which survived the disastrous events at the Mesozoic–Cenozoic boundary, experienced dramatic changes near the Paleocene-Eocene boundary due to the extinction of many species (Tjalsma and Lohman, 1983; Miller *et al.*, 1987).

Corfield (Corfield, 1987; Corfield and Shackleton, 1988) suggested a model of evolution for the early Paleogene planktonic foraminifers, according to which their evolutionary activity was controlled by changes in the surface water productivity and, as a consequence, by fluctuations in the intensity of the oxygen minimum zone. Different groups of foraminifers responded differently to such changes. However, the model does not eliminate the effect of temperature fluctuations on the evolutionary activity of foraminifers. The author emphasizes that the suggested model requires testing on other sections and in later intervals of the Paleogene.

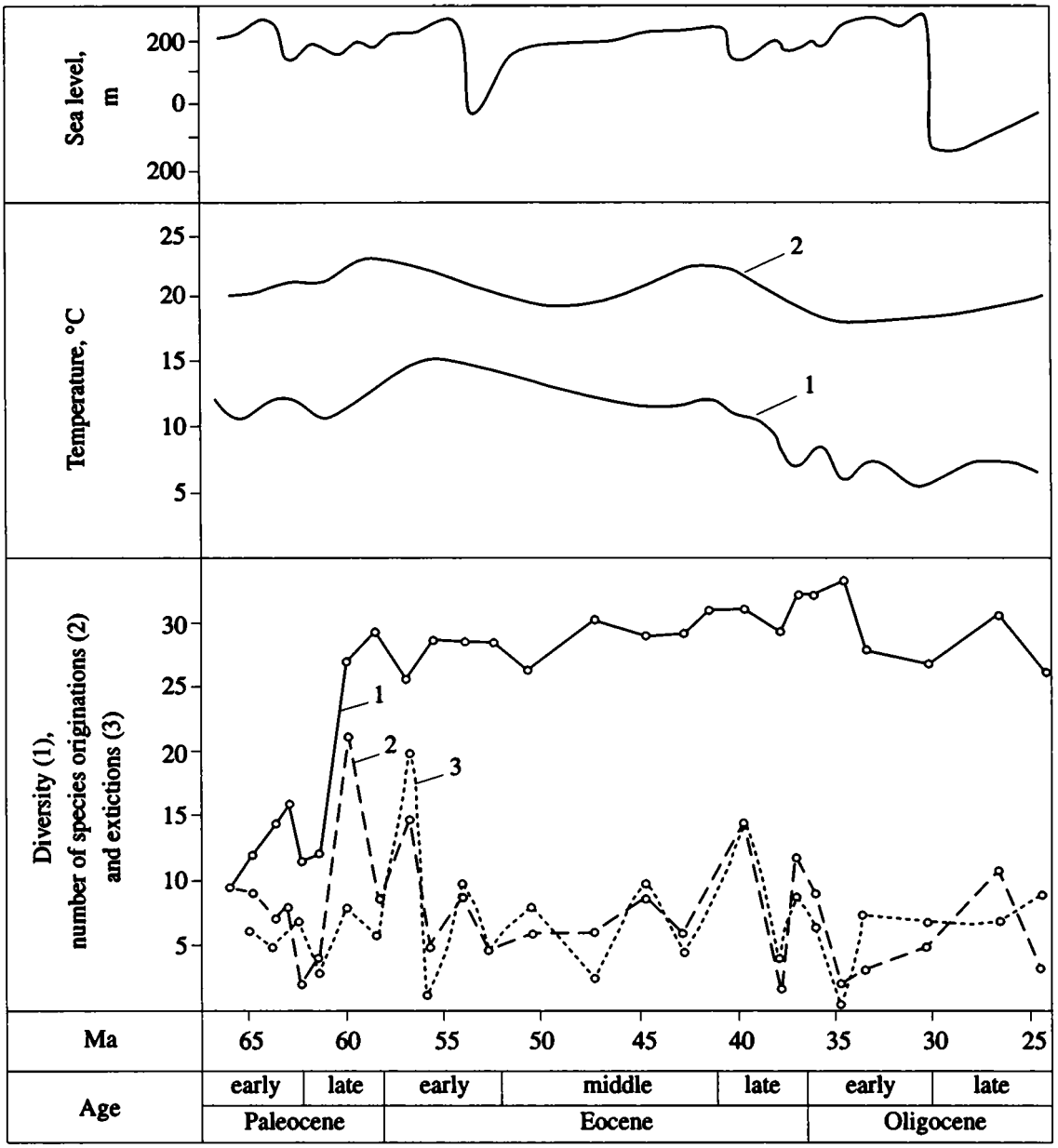

Fig. 3. *Correlation of faunal, climatic, and oceanological events in the Paleogene.*
Fluctuations in temperature of: 1 – bottom and 2 – surface water in the tropical Pacific after Douglas and Woodruff, 1981; sea-level changes after Vail and Hardenbol, 1979.

Activization of the evolutionary changes of planktonic foraminifers in the late Eocene–early Oligocene, following the relative deceleration in the early-middle Eocene, was synchronous with and apparently caused by global paleoceanological and paleoclimatic events occurring at that time. During this period, the northward motion of Australia and the simultaneous submergence of the South Tasmanian Ridge started. As a result, a deep connection between the Indian and Pacific oceans formed in the high latitudes, and the Circum-Antarctic current appeared, which resulted in thermal isolation of the Antarctic continent and in active ice sheet formation on its surface. It caused a decrease in surface and bottom water temperature during the late Eocene, and an even greater temperature drop at the boundary with the Oligocene (Shackleton and Kennett, 1975; Boersma and Shackleton, 1977; Vergnaud-Grazzini *et al.*, 1978; Shackleton and Hall, 1984; Shackleton *et al.*, 1984; Oberhänsli and Hsü, 1986), which was accompanied by the intensive formation of Antarctic bottom waters and the psychrosphere in the deeper parts of the ocean (Benson, 1975; Kennett and Shackleton, 1976), as well as by the growth of temperature gradients and the formation and setting of hydrological fronts.

The cooling in the late Eocene, especially at the boundary with the Oligocene, affected the low latitudes as well (Douglas and Woodruff, 1981). Detailed inves-

tigations (Keller, 1983b) revealed a more complex character of cooling there. By the ratio of surface, intermediate, and deep-water species of planktonic foraminifers in the Eocene complexes of the tropical Atlantic, Indian, and Pacific oceans, Keller revealed two periods of relatively high temperatures at the beginning and the end of the late Eocene on the background of progressive cooling in low latitudes. These periods are separated by a cool period. Surface dwelling species vanish, while the role of intermediate and deep-water species notably increases. This well correlates with curves of species origination and extinction compiled for the tropical-subtropical area of the Pacific. A considerable decline in temperatures at the middle-late Eocene boundary, and the oceanological reorganization, which resulted in the formation of a water mass structure in the Oligocene and Miocene analogous to the present, determined the cardinal changes in the planktonic foraminifer fauna. In consequence, many species became extinct. The most dramatic changes occurred at the middle-late Eocene boundary (the boundary of the *Truncorotaloides rohri* and *Globigerapsis semiinvoluta* zones). Many species (15) died out at that time, and even entire ecological types vanished (keeled globorotaliids, acarininids, truncorotalloids, many hantkeninids), which were characteristic of the warm-water environment. The vacated ecological niche was populated in the earliest late Eocene (the *Globigerapsis semiinvoluta* Zone) by a new foraminifer association consisting of cooler-water species. A slight increase in temperature of surface water after a considerable drop at the middle-late Eocene boundary, which was registered on the isotopic curves, promoted the species origination process. During this time, 15 new species appeared.

In the middle-late Eocene (the *Globorotalia cocoaensis* Zone) the evolutionary activity of foraminifers decreased notably on the background of the surface water temperature drop. This moderated the species origination process.

Termination of the late Eocene is marked, in addition to a slight warming, by a notable outburst of evolutionary activity, accompanied by the extinction of many foraminiferal taxa, both of species that played an important role in the middle Eocene, and of those that appeared in the earliest late Eocene. This stage apparently represents the adaptation of foraminifers to the advancing decrease in temperature and the development of a new foraminiferal association, which came to dominate in post-Eocene time. In the late Eocene, species origination accelerated in conjunction with a relative rise in temperatures. In total, 21 species appeared in the latest Eocene and at the boundary with the Oligocene (the *Globigerina gortanii–Globorotalia centralis* and *Globigerina tapuriensis* zones). Typical Oligocene forms can be found among them, such as *Globorotalia gemma, G. munda, Globigerina ampliapertura, G. angiporoides, G. officinalis, G. praebulloides, Cassigerinella chipolensis*, and others. According to Keller's data (1983b) at that time, the role of surface dwelling species of planktonic foraminifers also increased notably, having bean insignificant in the middle-late Eocene.

Acceleration of species origination is also recorded in the late Oligocene, at the *Globorotalia opima* and *Globigerina ciperoensis* zones boundary, when 11 new species appeared, most of which became an integral part of the Miocene fauna. This sharp increase also agrees in time with the rise in sea level (Vail and Hardenbol, 1979) and with a relative warming, which, as a rule, is not registered by isotopic data, but is well expressed in the relative increase in planktonic foraminifer diversity in the Australia–New Zealand region (Jenkins, 1973; Krasheninnikov *et al.*, 1988). This increase is also expressed in the migration of warm water association of nannofossils and planktonic foraminifers into high latitudes (Haq *et al.*, 1977), as well as in the increased role of surface dwelling species of planktonic foraminifers in the tropical area of the ocean (Keller, 1983b).

CONCLUSION

The analysis of species diversity changes in zonal complexes of planktonic foraminifers in the Paleogene sediments of the tropical-subtropical area of the Pacific, and of their evolutionary activity throughout the Paleogene allows us to conclude the following:

(1) In the Paleogene, on the background of a historically rapid evolutionary change in foraminifer associations, periods of increased evolutionary activity of planktonic foraminifers can be distinguished. This is manifested by an increase in the rate of species origination with a synchronous or subsequent extinction of many species.

(2) This is more strikingly manifested in the late Paleocene–early Eocene (the interval of the *Globorotalia pseudomenardii–Globorotalia subbotinae* zones). The high evolutionary activity of planktonic foraminifers was also recorded in the late Eocene and at the boundary with the Oligocene (the interval of *Globigerapsis semiinvoluta–Globigerina gortanii–Globorotalia centralis* zones). In the late Eocene, two episodes of acceleration in the rate of species origination and extinction are marked, in the beginning (the *Globigerapsis semiinvoluta* Zone), and at the end of the Eocene (the *Globigerina gortanii–Globorotalia centralis* Zone), which are divided by a short period of attenuation of evolutionary renovation of foraminiferal associations. A relative burst of species formation also occurred in the second half of the late Oligocene (the *Globigerina ciperoensis* Zone).

(3) All three periods of increased rates of species origination and (generally) mass extinction of planktonic foraminifers are synchronous with major climatic and oceanological events caused by tectonic reorganization, the evolution of the Antarctic ice sheet, and sea-level fluctuations.

(4) Planktonic foraminifer diversity changed insignificantly in the warm water area of the Pacific after an abrupt increase in the early and in the second half of the late Paleocene, and after a relative decrease in the middle Paleocene and at the Paleocene-Eocene boundary, to reach a maximum in the latest Eocene–earliest Oligocene. In the Oligocene, a maximal diversity on the background of relatively low values is recorded in the middle early Oligocene (the *Globigerina sellii* Zone) and in the second half of the late Oligocene (the *Globigerina ciperoensis* Zone).

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Paleogene–Neogene Boundary Layers in Northwestern Sakhalin

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Abstract – The lithological composition of the bed lying between the Khoindzho (Oligocene) and Upper Due (Miocene) formations was considered, and its paleontological characteristics were given. Sedimentation hiatuses, established at the Paleogene–Neogene boundary in the considered region, hinder the identification of this boundary position. Recent evidences from the Markevich Cape beds suggest their early Miocene age.

In the Aleksandrov and northern Uglegorsk regions, on the western coast of Sakhalin, the Paleogene–Neogene boundary occurs within the unit found between the regional volcanic Khoindzho and the terrigeneous coal-bearing Upper Due Formations (Krasilov and Kundyshev, 1982; Khudik, 1985). This boundary unit, with a complicated composition and a thickness ranging from several dozen to several hundred meters, has long attracted the attention of geologists. Recently, interest in it has increased. In connection with the regional conference on stratigraphy, presently being prepared, the succession and the age of layers in the complex are to be defined precisely. Investigations into IGCP Project no. 326, "Oligocene–Miocene Transition in the Northern Hemisphere" have started. Finally, a publication (Fot'yanova and Serova, 1987) has appeared, containing data on this unit that were used to confirm the existence of the late Miocene climatic optimum.

The boundary layers were first described in 1927 by P.I. Polevoi, who united them under the name Khoindzho–Kirpich coal-bearing formation. Later it was discovered that he had assigned to these layers both the intermediate strata itself and the lower beds of the Upper Due Formation (in their present volume). In addition, the rocks were referred to as the "basaltic tuffoid horizon" (after A.A. Kapitsa) and the Markevich Cape layers (after B.M. Shtempel'). Later, the intermediate strata section was complemented by the Brodyazhka Beds (Resheniya...,1961). The investigations on Paleogene–Neogene sequences in the southern parts of the island made it possible to distinguish formations of South Sakhalin nomenclature in the boundary layers (Geologicheskaya Karta..., 1977).

The boundary layers are discreetly spread over the shoreline from the Uandi Cape in the north to the southern border of the Aleksandrovsk region (Pil'vo). They can also be traced further to the south, to Lesogorsk settlement, where the Aleksandrovsk type of the section of the Paleogene-Neogene deposits is preserved. Their structure varies from place to place. In the Uandi and Boshnyak capes (Fig. 1), the Upper Due Formation rests on the basalts (member 3), which overlie strata of clayey cherts with interbeds of psephitic tuffs, lithologically resembling the Dae-Khurie Formation in Northern Sakhalin (in the section extending along the Srednii Vagis River) and the Nevel'sk–Kholmsk Formation, situated in the south. The thickness of the Upper Due Formation is nearly 250 m. The unit lies on a thin (25 m) basal member of clayey sandstones mixed with gravel and pebbles (member 1) unconformably overlying Upper Cretaceous deposits. Palynological data suggest the Oligocene age of the cherty strata and their basal member.

To the north of the Uandi Cape. There are no tuffites or effusives of the Khoindzho level. The Upper Due Formation, with its characteristic palynocomplex, occurs directly on Upper Cretaceous rocks.

In the northern part of the Khoindzho Cape, a member of tuff conglomerates with sandstone interbeds and a thin layer of carbonaceous argillite (member 1) lies on massive tuffs of the Khoindzho Formation (stratotype) (Fig. 1). The member is 12 m thick. Identified higher up are interbedded sandstones and clayey siltstones (member 2), from which fauna and partly flora were collected. Its thickness is 13 m. It is overlain with a hiatus by basal conglomerates of the Upper Due Formation.

Though the succession of layers is clearly distinguished, the paleobotanic interpretations vary. In the transition layers, L.I. Fot'yanova (Fot'yanova and Serova, 1977) has identified small-leaved and, in the Upper Due Formation, broad-leaved flora. V.A. Krasilov and A.S. Kundyshev (1982) obtained the same results, attributing the former to the "cold Aquitanian" and the latter to the "warm Burdigalian." However, in the lower part of the Upper Due Formation, M.A. Akhmet'ev (1976) also identified the cryophilic-mesophilic flora of the Aniai type and established that 150 m higher, the section gave way to the thermophilic-mesophilic flora of the Daijima type.

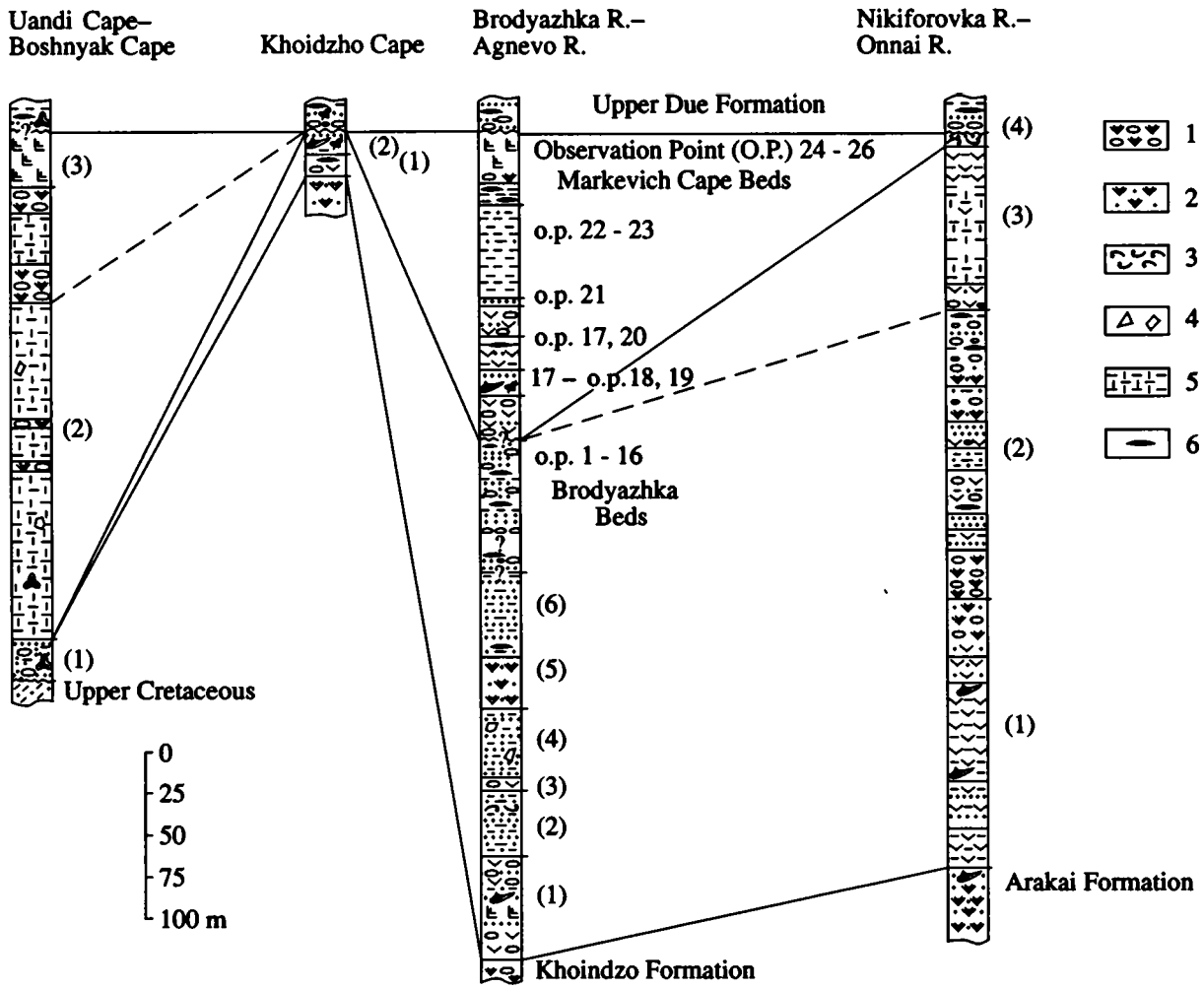


Fig. 1. *Correlation scheme of the boundary beds sections.*
1 – Psephitic tuff; 2 – psammitic tuff; 3 – shell rock; 4 – fragments of effusives; 5 – cherty claystone; 6 – coal, clayey rock.

Marine fauna was collected from the boundary layers in the Khoindzho Cape (Istoriya..., 1963) and dated by T.G. Kalishevich. V.D. Khudik (1985), who supplemented the list of mollusks, believes that the fauna suggests the Oligocene age.

In the northern part of the Uglegorsk area, a section of boundary beds is exposed near Boshnyakovo settlement along the Nikiforovka, Avgustovka, and Onnai rivers. Here, green psammitic basaltic andesite tuffs of the Khoidzho (Arakai) Formation are overlain by a member 1 of alternated sandy tuff siltstone, sandy and siltytuffites; and occasionally, tuffs with remnants of marine mollusks. The member is 120 - 190 m thick. Still higher, a member 2 of coarse-grained rocks is identified: psephitic and psammitic tuffs, tuff conglomerates, tuffstones with interbeds of siltstone, claystone, carbonaceous claystone and ash coal. The member is 150 - 200 m thick.

There is no consensus on the stratigraphic position of these two members. V.I. Golovinskii and L.S. Margulis, who investigated the section, attributed them to different levels: the former referred them to the Kholmsk Formation, the latter, to the Arakai Formation.

Further in succession there is a member 3 of light-colored stratified cherty claystones with interbeds of tuffstones. Its thickness is 100 - 200 m. The section terminates in a member 1 of dark claystones with interbeds of sandstones. The thickness of the member reaches 50 m. It contains mollusk remnants rich in *Mya* forms. The member is discordantly overlain by the Upper Due Formation.

The lithology of the cherty member and its position in the section leave no doubt that it is an analog of the Kholmsk or Nevel'sk formations, or of both. It may be surmised that it belongs to the Nevel'sk–Chekhov level.

The total thickness of the deposits between the Arakai tuffs and the Upper Due Formation is about 400 m.

The most controversial is a series of boundary layer outcrops on the coast between the Brodyazhka and Agnevo Rivers. A.N. Krishtofovich (1927, 1932), one of the first investigators of the region, suggested, based on the visible succession of layers in the Agnevo

region, that the coastal tuff bed and the overlying variegated formation (of the Markevich Cape) are the highest parts of the stratigraphic section. The flora collected and described by M.O. Borsuk was in agreement with this assumption. E.M. Smekhov (1941, 1953), who later investigated the Aleksandrov region, accepted Krishtofovich's point of view. He located the variegated formation over the unconsolidated tuffs, i.e. well above the Upper Due Formation, relying on "young" flora and the age datings, made by A.P. Il'ina using mollusks.

A large-scale geological survey was carried out in the coastal part of the region in the late 1930s and early 1940s. The results of the survey indicated a doubling of the section of the Paleogene–Neogene deposits along the upthrow or overthrust in the area between the Doctorskaya River in the north and the Porlongi River in the south. Here, along the submeridional fault, the Khoindzho, Upper Due, and Unconsolidated formations are in contact with the Gennoishi and Khoindzho formations lying to the west. On the shore there are outcrops of the upper beds of the Hoindzho formations and the transitional unit.

In addition, F.G. Lautenshleger collected fauna, which enabled him to assign the transitional beds to the lowermost parts of the Upper Due Formation. Unfortunately, the results of his research remain unpublished, and reports, which are difficult to procure, were underused.

Nevertheless, in the scheme adopted by the 1959 Okha Conference on Stratigraphy, and substantiated by the observations made by I.I. Ratnovskii during field trips, two units, the Brodyazhka and the Markevich Cape beds, have been distinguished between the Ust'-Agnevo tuffs of the Khoindzha Formation and the Upper Due Formation. The former was identified as the upper subformation of the Khoindzho Formation, and the latter was recognized to be an independent (Agnevo) Formation. Later, Ratnovskii (1969) included all the transitional strata into the Khoidzho Formation.

While compiling the State Geological Map (Sheet M-54-XVII), A.S. Shuvaev and M.Z. Bakhteeva adopted an old (1959) scheme of boundary beds sequence, which attributed the Brodyazhka complex to the Kholmsk Formation, and the Markevich Cape strata to the Chekhov Formation. They described the following section of the Brodyazhka beds, from bottom to top (see Fig. 1):

(1) Tuff conglomerates intercalated with basalts; the upper part contains interbeds and lenses of sandstones and interbeds of siltstones with fauna. Thickness: 60 m.

(2) Siltstones with interbeds of sandstones and shells. Thickness: 40 m.

(3) Tuff conglomerates. Thickness: 8 m.

(4) Interbedded siltstones and sandstones; occasional beds contain blocks of andesites and basalts. Thickness: 35 m.

(5) Tuffs. Thickness: 30 m.

(6) Siltstones and sandstones, similar to those of member 4 with interbeds (up to 0.5 m) of coaly claystones in the lower part. Thickness: 50 m.

Recently, new data were obtained on the flora of the Markevich Cape Beds (Krasilov and Kundyshev, 1982; Akhmet'ev, 1978), which confirmed its relationship with the flora of the Upper Due Formation.

Recently, however, Krishtofovich–Smekhov's version was unexpectedly supported. On the basis of samples collected by L.I. Fot'yanova, M.Ya. Serova identified a "young" complex of foraminifers in the beds of the Markevich Cape.

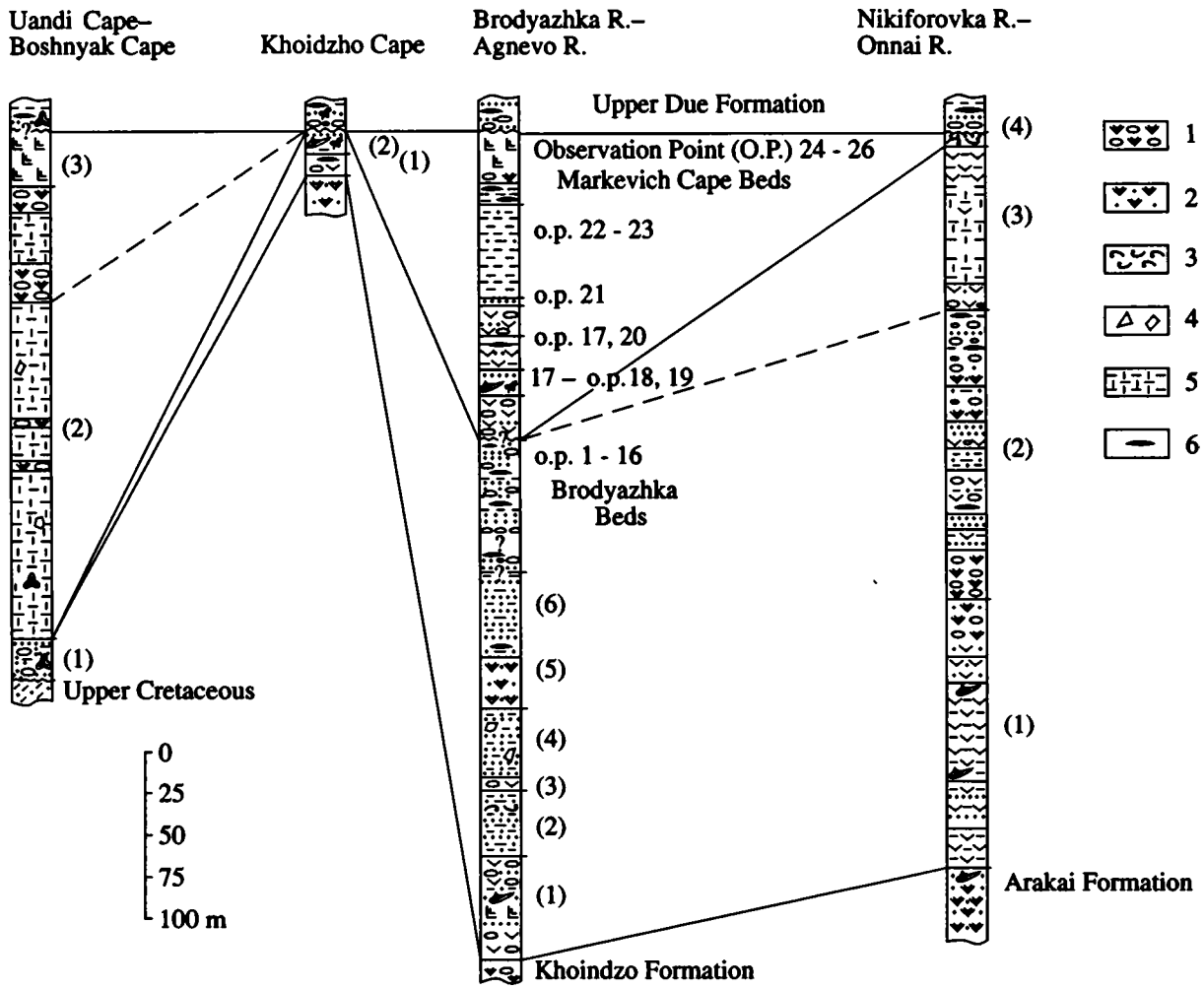
Keeping in mind that a return to the previous concept contradicts all other geological and biostratigraphic information, we conducted additional field observations within the Markevich Cape area and received new paleontological evidence confirming that the Markevich Cape Beds belong to the lower and not to the upper Miocene deposits.

A section of terrigenous, volcano-terrigenous, and volcaniclastic deposits of different dimensions, from conglomerates to siltstones, was exposed in the southern part of the Markevich Cape (Fig. 2). At the cape itself, these deposits are covered by basalts. A "hot" contact is recorded accompanied by the formation of underlying clayey rocks burnt to terracotta. The beds dip west-northwestward at angles from 10° to 70°. Fractures of an unclear type are observed.

Basalts in the northern part of the cape are overlain evidently unconformably by the Upper Due Formation.

The section can be subdivided into several members. The lowest member (observation points 1 - 16) is exposed at the foot of a coastal slope in the southern part of the section. It is represented by the interbedding of thick (5 - 15 m) layers of light-colored, presumably tuffaceous, sandstones with different grain size, which contain gravel and pebbles, and thin (up to 2.5 m) layers of dark claystones with interbeds of coaly claystones in the roof. Remnants of leaves and coarse plant detritus are also encountered. The rocks comprise numerous rounded fragments of light-colored aphanitic, evidently, effusive rocks. The visible thickness is 80 m. The base of the member is hidden. The contact with the next member is completely covered with talus. This member may be assigned to the Brodyazhka layers. The examined samples from the member (o.p. 2 and 9) are marked by the predominance of coniferous pollen, the most significant of which are various species of the *Tsuga* genus (including *Ts. parva* Brutm, *Ts. torulosa* (Zakl.) Brutm.) The composition of angiosperm pollen and spores is extremely impoverished and their abundance is insignificant. Such spectral character is consistent with the Central Tamlevo Oligocene palynocomplex of the *Podocarpus totara* and *Tsuga parva* palynozone (Brutman, 1983).

The three following members, belonging exclusively to the Markevich Cape Beds, are exposed in an escarpment further to the north. The lowest of them is composed of brown psephitic and psammitic tuffs and



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1 – Psephitic tuff; 2 – psammitic tuff; 3 – shell rock; 4 – fragments of effusives; 5 – cherty claystone; 6 – coal, clayey rock.

Marine fauna was collected from the boundary layers in the Khoindzho Cape (Istoriya..., 1963) and dated by T.G. Kalishevich. V.D. Khudik (1985), who supplemented the list of mollusks, believes that the fauna suggests the Oligocene age.

In the northern part of the Uglegorsk area, a section of boundary beds is exposed near Boshnyakovo settlement along the Nikiforovka, Avgustovka, and Onnai rivers. Here, green psammitic basaltic andesite tuffs of the Khoidzho (Arakai) Formation are overlain by a member 1 of alternated sandy tuff siltstone, sandy and siltytuffites; and occasionally, tuffs with remnants of marine mollusks. The member is 120 - 190 m thick. Still higher, a member 2 of coarse-grained rocks is identified: psephitic and psammitic tuffs, tuff conglomerates, tuffstones with interbeds of siltstone, claystone, carbonaceous claystone and ash coal. The member is 150 - 200 m thick.

There is no consensus on the stratigraphic position of these two members. V.I. Golovinskii and L.S. Margulis, who investigated the section, attributed them to different levels: the former referred them to the Kholmsk Formation, the latter, to the Arakai Formation.

Further in succession there is a member 3 of light-colored stratified cherty claystones with interbeds of tuffstones. Its thickness is 100 - 200 m. The section terminates in a member 1 of dark claystones with interbeds of sandstones. The thickness of the member reaches 50 m. It contains mollusk remnants rich in *Mya* forms. The member is discordantly overlain by the Upper Due Formation.

The lithology of the cherty member and its position in the section leave no doubt that it is an analog of the Kholmsk or Nevel'sk formations, or of both. It may be surmised that it belongs to the Nevel'sk–Chekhov level.

The total thickness of the deposits between the Arakai tuffs and the Upper Due Formation is about 400 m.

The most controversial is a series of boundary layer outcrops on the coast between the Brodyazhka and Agnevo Rivers. A.N. Krishtofovich (1927, 1932), one of the first investigators of the region, suggested, based on the visible succession of layers in the Agnevo

region, that the coastal tuff bed and the overlying variegated formation (of the Markevich Cape) are the highest parts of the stratigraphic section. The flora collected and described by M.O. Borsuk was in agreement with this assumption. E.M. Smekhov (1941, 1953), who later investigated the Aleksandrov region, accepted Krishtofovich's point of view. He located the variegated formation over the unconsolidated tuffs, i.e. well above the Upper Due Formation, relying on "young" flora and the age datings, made by A.P. Il'ina using mollusks.

A large-scale geological survey was carried out in the coastal part of the region in the late 1930s and early 1940s. The results of the survey indicated a doubling of the section of the Paleogene–Neogene deposits along the upthrow or overthrust in the area between the Doctorskaya River in the north and the Porlongi River in the south. Here, along the submeridional fault, the Khoindzho, Upper Due, and Unconsolidated formations are in contact with the Gennoishi and Khoindzho formations lying to the west. On the shore there are outcrops of the upper beds of the Hoindzho formations and the transitional unit.

In addition, F.G. Lautenshleger collected fauna, which enabled him to assign the transitional beds to the lowermost parts of the Upper Due Formation. Unfortunately, the results of his research remain unpublished, and reports, which are difficult to procure, were underused.

Nevertheless, in the scheme adopted by the 1959 Okha Conference on Stratigraphy, and substantiated by the observations made by I.I. Ratnovskii during field trips, two units, the Brodyazhka and the Markevich Cape beds, have been distinguished between the Ust'-Agnevo tuffs of the Khoindzha Formation and the Upper Due Formation. The former was identified as the upper subformation of the Khoindzho Formation, and the latter was recognized to be an independent (Agnevo) Formation. Later, Ratnovskii (1969) included all the transitional strata into the Khoidzho Formation.

While compiling the State Geological Map (Sheet M-54-XVII), A.S. Shuvaev and M.Z. Bakhteeva adopted an old (1959) scheme of boundary beds sequence, which attributed the Brodyazhka complex to the Kholmsk Formation, and the Markevich Cape strata to the Chekhov Formation. They described the following section of the Brodyazhka beds, from bottom to top (see Fig. 1):

(1) Tuff conglomerates intercalated with basalts; the upper part contains interbeds and lenses of sandstones and interbeds of siltstones with fauna. Thickness: 60 m.

(2) Siltstones with interbeds of sandstones and shells. Thickness: 40 m.

(3) Tuff conglomerates. Thickness: 8 m.

(4) Interbedded siltstones and sandstones; occasional beds contain blocks of andesites and basalts. Thickness: 35 m.

(5) Tuffs. Thickness: 30 m.

(6) Siltstones and sandstones, similar to those of member 4 with interbeds (up to 0.5 m) of coaly claystones in the lower part. Thickness: 50 m.

Recently, new data were obtained on the flora of the Markevich Cape Beds (Krasilov and Kundyshev, 1982; Akhmet'ev, 1978), which confirmed its relationship with the flora of the Upper Due Formation.

Recently, however, Krishtofovich–Smekhov's version was unexpectedly supported. On the basis of samples collected by L.I. Fot'yanova, M.Ya. Serova identified a "young" complex of foraminifers in the beds of the Markevich Cape.

Keeping in mind that a return to the previous concept contradicts all other geological and biostratigraphic information, we conducted additional field observations within the Markevich Cape area and received new paleontological evidence confirming that the Markevich Cape Beds belong to the lower and not to the upper Miocene deposits.

A section of terrigenous, volcano-terrigenous, and volcaniclastic deposits of different dimensions, from conglomerates to siltstones, was exposed in the southern part of the Markevich Cape (Fig. 2). At the cape itself, these deposits are covered by basalts. A "hot" contact is recorded accompanied by the formation of underlying clayey rocks burnt to terracotta. The beds dip west-northwestward at angles from 10° to 70°. Fractures of an unclear type are observed.

Basalts in the northern part of the cape are overlain evidently unconformably by the Upper Due Formation.

The section can be subdivided into several members. The lowest member (observation points 1 - 16) is exposed at the foot of a coastal slope in the southern part of the section. It is represented by the interbedding of thick (5 - 15 m) layers of light-colored, presumably tuffaceous, sandstones with different grain size, which contain gravel and pebbles, and thin (up to 2.5 m) layers of dark claystones with interbeds of coaly claystones in the roof. Remnants of leaves and coarse plant detritus are also encountered. The rocks comprise numerous rounded fragments of light-colored aphanitic, evidently, effusive rocks. The visible thickness is 80 m. The base of the member is hidden. The contact with the next member is completely covered with talus. This member may be assigned to the Brodyazhka layers. The examined samples from the member (o.p. 2 and 9) are marked by the predominance of coniferous pollen, the most significant of which are various species of the *Tsuga* genus (including *Ts. parva* Brutm, *Ts. tcrulosa* (Zakl.) Brutm.) The composition of angiosperm pollen and spores is extremely impoverished and their abundance is insignificant. Such spectral character is consistent with the Central Tamlevo Oligocene palynocomplex of the *Podocarpus totara* and *Tsuga parva* palynozone (Brutman, 1983).

The three following members, belonging exclusively to the Markevich Cape Beds, are exposed in an escarpment further to the north. The lowest of them is composed of brown psephitic and psammitic tuffs and

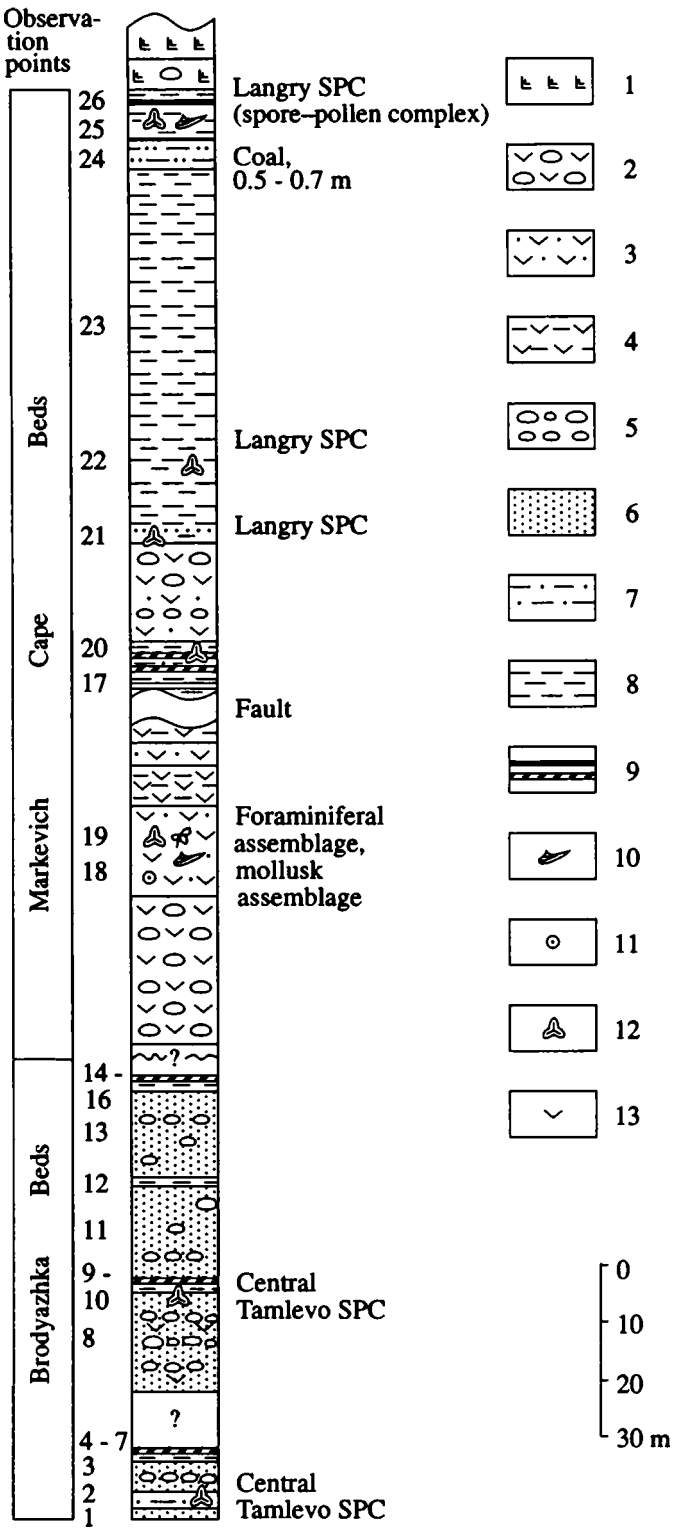

Fig. 2. *The Paleogene–Neogene section in the southern part of the Markevich Cape.*

1 – basalt; 2 – tuff conglomerate; 3 – tuffstone; 4 – tuff siltstone; 5 – conglomerate, gravelite; 6 – sandstone; 7 – siltstone; 8 – claystone; 9 – coal, carbonaceous claystone; 10 – mollusk fauna; 11 – microfauna; 12 – spores and pollen; 13 – volcanic material admixture.

tuffites. The rocks contain fragments of large trunks. The visible thickness is 30 m.

The intermediate member is 40 m thick and is represented by interbedded tuffstones and tuff siltstones, comprising remnants of different fauna and flora. Nearly all fossils were collected from rocks of this member (Fig. 2, o.p. 17 - 20).

Unlike the previous samples, those taken from this member (o.p. 19 and 20) are characterized by the enriched composition of the angiosperm pollen. Pollen of thermophilic plants (mostly *Juglans* sp.; in lesser amounts, *Fagus* sp.; pollen of the subtropical *Rhus* sp., *Liquidambar* sp. and occasionally, *Symplocos* sp.) and the Pinaceae fam., is predominant; the role of *Tsuga* pollen in the latter is persistently significant. The replacement of *Ts. parva* by *Ts. sauerae* Brutm. pollen is characteristic. All of this suggests a close relation to the Berezovka palynocomplex, which characterizes the deposits of the lower part of the *Ceratopteris*, *Tsuga sauerae*, and *Trapa comitantiborealis* palynozone of early Miocene.

A fairly thermophilic foraminiferal assemblage was encountered at observation point 19. It is represented by rare specimens of the following species: *Quinqueloculina seminula* L., *Guttulina* sp. indet. *Polymorphina* sp., indet., *Discorbis janus* Volosh, *Nonion nagasawaensis* Matsunaga, *Perfectononion* aff., *praeincertus* Kuzn., needles of sea urchins, and *Placentamina* sp.

A similar, though more diverse, assemblage of foraminifers was identified in Sakhalin at the Chekhov Formation level along the Arkanzas River, and in borehole I of the southwestern shelf in the Krasnogorsk area within the 2200 - 2359 m depth interval, in the deposits of the undifferentiated Upper Due and Chekhov formations. An assemblage (Atlas..., 1984) with *Discorbis janus* from the Tochilino reference section in Kamchatka was described by M.Ya. Serova from the Il'ina Formation.

The upper member is composed of brown tuff conglomerates. Its thickness is 20 m. A thin intercalation of sandy and silt-clayey rocks, several meters thick, is recorded in the member top (o.p. 21)

The uppermost parts of the section (o.p. 22 - 26) are exposed at the base of a minor slope, terminating in the Markevich Cape. They are composed of dark gray massive claystones and fine-grained siltstones, with rare thin interbeds of lighter coarse-grained siltstones and two coal beds in the upper part. The thickness of the member is 80 m. The thickness of the whole section (with the exception of the cape basalts) is 170 m.

The spore-pollen spectra of samples from o.p. 21, 22, and 26 are similar in composition. Only the spectrum of a sample from point 22 has a greater amount of *Pinus* pollen. Pollen species of Juglandaceae (*Juglans* sp., *J. gracilis* Anan., *J. polyporata* Vojc., *Carya* sp.) and Fagaceae (*Fagus grandifoliiformis* Pan., *F. japoniciformis* Anan., *F.* sp., *Quercus* sp.) are dominant. Pollen of subtropical *Nyssa* sp., *Liquidambar* sp., *Rhus* sp., Rutaceae gen. indet., is identified. *Trapa comitanti-*

borealis Brutm. and *Tsuga sauerae* Brutm. are encountered in all the samples, indicating a similarity to the Langry spore-pollen assemblage of the palynozone *Ceratopteris*, *Tsuga sauerae*, and *Trapa comitantiborealis* of early Miocene.

Mollusk remnants have been identified at o.p. 19, among them, *Mytilus* (*Mytiloconcha*) *expansus* Arn., *Mytilus* sp., *Modiolus* ex gr. *angulatus* Slod., *Chlamys* ex gr. *kaneharai* (Yok.), *Ostrea* sp., *Pitar* cf. *kavranensis* Slod., *Pitar* aff. *tatarica* Laut., *Pitar* sp., *Macrocallista*? *markewitschi* Laut., *Saxidomus*? *arnieansis* (Sim.), *Saxidomus*? *sakhalinensis* (Sim.), *Lucinoma acutilineata* (Conr.), *Diplodonta sertunayensis* (Kog.), *Keenocardium* cf. *californiense* (Desh.), *Clinocardium shinjiense* (Yok.), and *Macoma* sp.

Due to an abundance, Mytilidae (*M. exspansus*, *M. ynezianus*) are best represented in this complex. In California, their occurrence is assigned to the lower Miocene Vaqueros Formation, whereas in Western Kamchatka (beds with *M. exspansus*), it is assigned to the Etolona Formation (Atlas..., 1984). Pectinidae (*Chlamys kaneharai*) are known in numerous Miocene sequences in Japan, in the Chekhov Formation in Sakhalin, and in the Kuluven and Il'ina formations in Western Kamchatka. The appearance of relatively "young" species in the assemblage (*K. californiense*, *D. sertunayensis*, *Cl. shinjiense*) is recorded at the Bora level, except for *Pitar kavranensis*, which has been known from the Uglegorsk (Ausi) time.

As was already mentioned, Simonova, who investigated mollusk fauna from the Markevich Cape, using the samples collected by Krishtofovich from 1917 to 1927, suggested a late Miocene or, more likely, Pliocene age for the mollusk-bearing tuffogenic sandstones. Fauna collected later and studied by Lautenschleger, enabled him (in 1952) to conclude that tuffogenic sandstones with fauna belonged to the lowermost parts of the Upper Due Formation and that they had appeared in the middle Miocene. He regarded as synchronous the Nevel'sk Formation and a lower part of the Uglegorsk Formation in Southern Sakhalin. Further studies of the Markevich Cape fauna by Kuzina (1961) and Krishtofovich (1961) suggested that it may be of the Chekhov time. At the present stage in our knowledge of the mollusk fauna of the Markevich Cape, above conclusions seem to be the most acceptable. Evidently, its probable age may be limited to the early middle Miocene.

So, the upper part of the Oligocene Brodyazhka Beds, the lower Miocene beds of the Markevich Cape, and the lower part of the lower-middle Miocene Upper Due Formation were exposed in the shoreline section of the Markevich Cape. No geological signs of upper Miocene deposits occurring here were revealed[1].

In the entire region under consideration, we can identify three horizons of deposits between the Khoidzho tuffs or their analogues and the Upper Due Formation: upper Arakai, Kholmsk–Nevel'sk, and Chekhov, assuming that a subdivision between the latter is marked by the appearance of abundant volcanic material of basic composition. The Brodyazhka Beds belong to the first horizon. The cherty beds occurring in the Boshnyak sections and in the Boshnyak Cape can be attributed to the second and third horizons. Most likely, the part of the Brodyazhka beds where rocks of the "Kholmsk" appearance are encountered can be assigned to them as well. The Markevich Cape Beds correspond to the third horizon.

Evidently, deposits of the three horizons are divided by stratigraphic unconformities; as a result, certain sections lack certain elements of the general succession. In the Boshnyak and Uandi capes area there are no Brodyazhka Beds (Fig. 1); and in the Khoindzho Cape area they are preserved only in part. The Kholmsk and Nevel'sk horizons are missing in the Brodyazhka–Agnevo section (or their siliceous-clayey deposits are replaced by coarse-grained ones). The Markevich Cape Beds are nearly absent in the Boshnyak section, except for a thin member of interbedded sandy and clayey rocks with abundant *Mya* species, which may conventionally be assigned to these beds.

As may be inferred from the available data, the Brodyazhka Beds and the cherty unit are Oligocene, whereas the Markevich Cape beds are Miocene deposits. This enables us to draw several conclusions. If the correlation of basalts from the Uandi and Boshnyak capes with effusives from the Markevich Cape is correct, the Paleogene–Neogene boundary of the Boshnyak Cape should be drawn in the upper part of the cherty unit. The Khoidzho Cape section cannot be used as a site to clarify the position of the Paleogene–Neogene boundary, as there is a great hiatus within the transitional beds here. To define the exact position of the boundary in a continuous section, we should thoroughly investigate the upper part of the corresponding beds in the Boshnyak area.

[1] The evidence from the Aleksandrov marine borehole suggests that these deposits (the Maruyama Formation) are represented by slightly consolidated terrigenous rocks of sand-clayey lithology.

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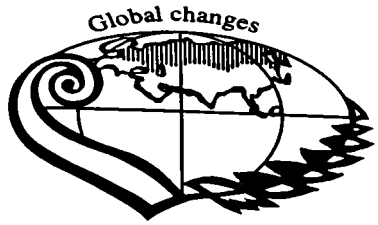

Evolution of the biosphere

The Early Villafranchian Stage in the Development of the Mammalian Fauna of Northern Eurasia

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Abstract – An analysis of the Pliocene faunas of the middle latitudes of Eurasia in combination with climatic, paleomagnetic, and radiometric evidence and data on world ocean eustatic fluctuations has shown a synchronism of the main faunal changes and global climatic events. The most considerable renewal of the generic composition occurred at the early–late Pliocene boundary (in the interval 3.8 - 3.5 Ma).

INTRODUCTION

The most important climatic events at the end of the early Pliocene and beginning of the late Pliocene correspond to the time intervals of 3.8 - 3.5, 3.2 to 3.1, and 2.5 to 2.4 Ma, which reflect global coolings of an increasing amplitude (Shackleton and Opdyke, 1977). The essential changes of mammal fauna, i.e., the extinction or migration of the most thermophilic species and the appearance of the more cryophilic ones are confined to these periods. The increasing aridity during the cooling in the temperate latitudes led to the distribution of animals over the open landscape. The formation of land bridges between the continents during the drop in the world ocean levels in the intervals 3.8 - 3.6 and 2.9 to 2.8 Ma (Haq *et al.*, 1987) gave rise to an influx of immigrants (Lyndsay *et al.*, 1980).

By the beginning of the late Pliocene, Villafranchian fauna had appeared in West Europe. The time span of its early stage (zone MN 16; Mein, 1990), containing a great number of Ruscinian elements, is estimated by different researchers to range from 1.1 - 1.6 Ma. The lower and upper limits of this stage have no clear age determination – the following data are suggested: from 4.1 - 3.2 Ma for the lower one and from 2.5 - 2.2 Ma for the upper.

LOWER VILLAFRANCHIAN BOUNDARY: THE WEST EUROPEAN FAUNA OF THE FIRST HALF OF THE EARLY VILLAFRANCHIAN

The Lower Villafranchian boundary in the Mediterranean is close to the Zanclean–Piacenze boundary (Rio *et al.*, 1991), correlating to the lower-upper Pliocene boundary, which coincides with the base of foraminifer zone N 20 and that of nannoplankton zone NN 16 (Berggren *et al.*, 1985).

The age of the lower Villafranchian boundary is defined based on comparison of the data from the type localities of the late Ruscinian (zone MN 15, Perpignana, France) and the first half of the early Villafranchian (MN 16a, Villafranca d'Asti, Italy), and also involves similar localities in southern West Europe, for which K-Ar and paleomagnetic ages have been obtained.

According to recent information, the Ruscinian–Villafranchian boundary falls in the interval of 3.8 - 3.4 Ma. The age of the Perpignan fauna is estimated by different scientists within the limits of 4.5 - 3.7 Ma. The reversely magnetized deposits of Perpignan are correlated with the Gilbert epoch (Lindsay *et al.*, 1990), either between the Cochiti episode and the Gauss epoch, or between the Sidufiall and Nunivak episodes (Clauzon *et al.*, 1990). Taking into account the data of B.U. Haq *et al.* (1987) on the world ocean eustatic fluctuations and correlations of the fossiliferous deposits of Perpignan with the eustatic cycle 3.5 (Clauzon *et al.*, 1990), we can agree that the fauna is most probably older than 3.8 Ma (Table 1).

The age of Villafranca d'Asti (Triversa) is additionally accepted as 3.05 - 3.01 Ma on the basis of an interpretation of the paleomagnetic results: the fossiliferous deposits have a normal polarity, they are included between reversely magnetized sediments, and are correlated with the Gauss epoch in the interval between the

Table 1. Correlation of late Ruscinian–early Villafranchian localities

Ages, Ma	Paleomagnetic scale	Continental scale	Zones	Glaciations: Arctic	Glaciations: Antarctic	Ocean level drops	West Europe	Romania	North shore of the Black Sea, Caucusus	Kazakhstan	Transbaikalia	Mongolia	China
2.48	Kaena Gauss	Villafranchian	16b				Monto-poli – / +	Cerna-testi +	Liven-tsovka I –				
							Rincon I + (2.6 - 2.7 Ma)	Podari +	Kvabebi +		Bere-govaya		Tunliu
							Etouaires						
							Villaroya						
							Vialette (3.3 - 2.6 Ma, 3.8 - 3.3 Ma)						Daodi +
2.92													
3.01	Mammoth						Triversa – / + / –	Covrigi Iaras 2+				Shamar (<3.1 ± 0.2 Ma)	
3.05													
3.15			16a										Yushe (Mazegou)
										Esekart-kan	Udun-ga		
							Layna +						
3.40										Ostraya Sopka –			
							Las Higueruelas (3.52 ± 0.45, 3.82 ± 0.34 Ma)		Odessa cata-combs –				Youhe
	Gilbert							Ciuper-ceni	Prut				Jingle
		Ruscinian	15					Malus-teni –					
3.86	Cochiti												
3.90							Perpignan –					Khirgis-Nur II + (lev. 51 - 55)	Gaozhu-ang + / – (Culiu-gou)

Mammoth and Kaena episodes (Azzaroli *et al.*, 1988; Lindsay *et al.*, 1980). The radiometric and paleomagnetic data on the localities in France (Vialette, Etouaires) and Spain (Layna, Las Higueruelas), which are close in age to Villafranca d'Asti, permit the suggestion that the lower age limit of the Early Villafranchian fauna is not older than 3.8 Ma and not younger than 3.4 Ma, and the upper limits of its early stage is not younger than 2.6 Ma. The age of the Etouaires fauna was determined to be within the limits of 3.4 - 3.1 Ma based on the K-Ar dating of underlaying tuffs of 3.5 - 3.4 Ma old (Bout, 1975). The K-Ar data of the Vialette fauna are 3.8 - 3.3 and 3.3 - 2.6 Ma, and those of the Las Higueruelas fauna are 3.82 ± 0.34 and 3.52 ± 0.45 Ma (Bout, 1975; Bandet *et al.*, 1978; Alberdi and Bonadonna, 1987). The normally magnetized deposits of Layna are referred to the beginning of the Gauss epoch or to the interval between the Mammoth and Kaena episodes (Aguirre and Morales, 1990; Azzaroli *et al.*, 1988).

A considerable fauna renovation occurred in the south of West Europe in the interval of 3.8 - 3.4 Ma. In the first half of the early Villafranchian not less than 10 genera of carnivores and artiodactyls (*Parameles*, *Euryboas*, *Megantereon*, *Homotherium*, *Lynx*, *Acinonyx*, *Arvernoceros*, *Leptobos*, *Gazellospira*, and *Pliotragus*) appeared; and three genera (*Dinofelis*, *Paracervulus*, and *Alephis*) disappeared (Table 2). Moreover, a great number of small mammals (*Galeryx*, *Trischizolagus*, *Occitanomys*, and others) became extinct.

Together with voles of the genus *Promimomys* (*P. cappettai*, *P. stehlini*, and *P. gracilis*) lacking tooth cement, which have those of the genus *Mimomys* (*M. polonicus* and *M. reidi*), having tooth cement, became widespread (Table 3). The index species for zone MN 16a was *P. cappettai* which replaced the characteristic upper Ruscinian *P. davakosi-occitanus*. *Hipparion crassum* was replaced by *H. rocinantis* (= *H. crusafonti*). The deer *Croizetoceros ramosus pyrenaicus* took the place of *C. ramosus ramosus*. During the transition from the Ruscinian to Villafranchian, the transformation of the species of rhinoceros from *Dicerorhinus miguelcrusafonti* to *D. jeanvireti*, bears from *Ursus ruscinensis* to *U. minimus*, hyenas from *Pachycrocuta pyrenaica* to *P. perrieri*, and canids from *Nyctereutes donnezani* to *N. megamastoides* occurred. The new forms coexisted with the Ruscinian species of mastodonts (*Anancus arvernensis* and *Zygolophodon borsonii*), primates, rhinoceros, tapirs, and others.

At the beginning of the early Villafranchian, the number of inhabitants of open landscapes together with animals adapted to more arid conditions (voles with tooth cement, *Chasmaporthetes*, *Acinonyx*, antilopes, and others), markedly increased. The faunal changes apparently began during the global cooling of the late Pliocene and the beginning of the early Pliocene. This was associated with an increase in the Antarctic ice cover at the 3.8 - 3.5 Ma period (Ciesielski and

Table 2. Distribution of large mammalian genera

Genera	15	16a	16b	17
Proboscidea				
Achidiskodon (Af)	?			
Carnivora				
Vulpes (A)				
"Canis" (A)				
Canis (A)				
Agriotherium				
Parameles				
Meles			?	
Talassictis				
Metailurus				
Dinofelis				
Megantereon				
Homotherium				
Lynx	?			
Acinonyx (Af)				
Perissodactyla				
Equus (A)	?			
Acerorhinus				
Coelodonta				
Postschizotherium				
Artiodactyla				
Metacervulus				
Eostyloceros				
Paracervulus				
Platycemas				
Procapreolus				
Capreolus				
Arvernoceros				
Orchonoceros				
Eucladoceros				
Libralces				
Leptobos				
Pliotragus				
Gazellospira				
Antilospiroides				
Antilospira				
Megalovis				
Synoryx				
Lyrocerus				
Tragocerus				
Alephis				

..... – *Mediterranean and European–Siberian subareas*

——— – *Central Asian subarea*

A – immigrants from America

Af – immigrants from Africa

Weaver, 1983). A decrease in the temperature of the oceans took place about 3.5 Ma ago. The fall of the World ocean level within the interval of 3.8 - 3.6 Ma (Haq *et al.*, 1987) led to the formation of a land bridge between Eurasia and America (Lindsay *et al.*, 1980). The cooling also affected the vegetation. At the Zanclean–Piacenze boundary in southern West Europe, the composition of the pollen flora changed: the abundance of Taxodiaceae decreased while the mesothermal and meso-microthermal elements and herbs increased in the spore-pollen spectra (Suc, 1990).

Italian researchers connect the formation of the Triversa fauna with the "Leptobos event," evidenced by an increase in aridity and cooling, which they correlate with a decrease in water temperature in the Mediterranean 3.2 to 3.1 Ma ago (Azzaroli *et al.*, 1988; Keigwin and Thunell, 1979). According to N.J. Shackleton and N.D. Opdyke (1977), the glacial-interglacial fluctuations, preceded by a period of stable interglacial or periglacial climate, began in the Northern hemisphere 3.2 Ma ago. The beginning of continental glaciation in the north of Eurasia is related to that level: in Iceland the glaciation is dated as 3.1 Ma old. This glaciation was accompanied by the greater fall in the level of the ocean in comparison with the preceding one (Haq *et al.*,1987). Approximately 3.1 Ma ago, the contrast between seasonal changes of climate increased in the Western Mediterranean (Suc, 1990).

Species found in the first half of the early Villafranchian in the Triversa fauna, include *Leptobos*, *Acinonyx*, *Homotherium*, and *Euryboas*. The presence of the Leptobos forms (*Chasmaporthetes*, *Hipparion fissure*, and others) in the deposits of a more ancient age (Las Higuerueles, Layna) allow us to state that the Leptobos event began approximately 0.3 - 0.5 Ma earlier.

WEST EUROPEAN FAUNA OF THE SECOND HALF OF THE EARLY VILLAFRANCHIAN

The type locality of the fauna of the second half of the early Villafranchian (subzone MN 16b) is Montopoly, Italy. The bone beds of sediments correlate with the base of the Matuyama epoch near the Gauss-Matuyama inversion (Lindsay *et al.*, 1980), but the lower age limit of this fauna may be more ancient (Azzaroli *et al.*, 1988). The datings on the Rincon I locality, Spain, close in age to Montopoli, and on some localities of the MN 17 zone (Poccaneyra and others), as well as certain climatic and eustatic indicators allow placing the boundary of subzones MN 16a and 16b within the time span of 2.6 - 2.7 Ma, and that of zones MN 16 and 17 slightly higher than the base of the Matuyama epoch. The age of the Rincon I locality is accepted as equal to 2.6 or 2.7 Ma based on paleomagnetic records (Azzaroli *et al.*, 1988; Aquirre and Morales, 1990). The K-Ar age of the Roccaneyra fauna is about 2.5 Ma (Bout, 1975).

The faunal changes at the boundary of the subzones MN 16a and 16b were caused mainly by an invasion of the *Archidiskodon*, *Equus*, and *Eucladoceros* forms and

Table 3. Stratigraphical range of species

Ruscinian	Villafranchian	
15	16a	16b
Promimomys davakosi-occitanus	*P. cappettai*	
	P. stehlini	
P. antiquus	*P. gracilis*	
	Mimomys polonicus	
	M. reidi	
	M. youhenicus	
	M. orientalis	
	M. bachiaonicus	
	Villanyia eleonorae	
Prosiphneus ericksoni	*P. praetingi*	
	P. paratingi	
	Elephas youheensis	*Archidiskodon rumanus*
		A. gromovi
Hipparion crassum		
	H. roscinantis (= H. crusafonti)	
H. houfenense (e.f.)	*H. houfenense* (l.f.)	
	H. pater	*H. sinense*
		Equus ex gr. *stenonis*
		E. livenzovensis
Dicerorhinus megarhinus		*D. etruscus*
		Coelodonta
Ursus ruscinensis–U. minimus		*U. etruscus*
Nyctereutes donnezani – N. megamastoides		
Pachycrocuta pyrenaica–P. perrieri		
	Chasmaporthetes lunensis	
	Acinonyx pardinensis	
	Megantereon megantereon (e.f.)	
	Lynx issiodorensis	
	Homotherium crenatidens	
Procapreolus wenzensis	*Capreolus* sp.n.	
Paracervulus australis		

Table 3. (Contd.)

Ruscinian	Villafranchian	
15	16a	16б
P. bidens		
Metacervulus capreolinus		
Eostyloceros maci		
Croizetoceros ramosus pyrenaicus	*C. ramosus ramosus*	
	Axis ubensis	
	A. shansius	
Cervus (Rusa) warthae	*C. pardiensis*	
	C. perrieri	
		Eucladoceros
	Arvernoceros ardei	
	Orchonoceros gromovi	
	Alcini gen. *indet.*	
	Leptobos stenometapon	
	Gazella sinensis	
	Antilospira zdanskyi	

by the wide occurrence of *Ursus etruscus* and *Dicerorhinus etruscus* over the territory of West Europe.

Genera *Archidiskodon* and *Equus* appeared approximately 4 Ma ago. The origin of elephants is considered to have occurred in Africa, and that of horses in America. It is supposed that elephants reached South Asia about 2.9 Ma ago and that horses migrated into Eurasia at about 2.6 Ma ago (Lyndsay *et al.*, 1980). The land connection between North America and Eurasia existed at the end of the Ruscinian, but the density of the horse population then was presumably insufficient for their dispersion. However, judging by data from East Europe and China, one cannot exclude the possibility that elephants and horses came into Eurasia at that time, though they did not play a noticeable role in the faunas until the second half of the early Villafranchian, and occupied only a few suitable geological niches.

The intensification of aridity and cooling at the end of the Gauss epoch led to the wide dispersion of inhabitants of open landscapes of the park and savanna types (elephants, horses, canids, *Dicerorhinus etruscus*, gazelles, and others), accompanied by the disappearance of a number of forest elements, characteristic of the fauna of the first half of the early Villafranchian (Azzaroli *et al.*, 1988). Those processes, occurring in the 2.5 - 2.4 Ma interval, were apparently related to the formation of the Arctic ice cover and an increase of the ice cover already existing in the Antarctic. The processes preceded the decrease of the ocean temperature. In Italy, this event is marked by the Aquatraversian erosional phase. At approximately that time, a large continental glaciation with the magnitude of about two-thirds of the maximal Pleistocene glaciation, began in the Northern hemisphere (Shackleton and Opdyke, 1977).

At the early-middle Villafranchian boundary, the genera *Clethrionomys*, *Meles*, and *Libralces* appeared, and *Parameles*, *Agriotherium*, and *Arvernoceros* disappeared. *Mimomys polonicus* was substituted by *M. pliocaenicus* and, in addition, the following transformations of species and subspecies took place: *Equus livenzovensis–E. stenonis vireti*, *Croizetoceros ramosus ramosus–C. ramosus medius* (in France), and *C. ramosus ramosus–C. ramosus pueblensis* (in Spain).

EARLY VILLAFRANCHIAN FAUNAS OF THE EAST MEDITERRANEAN PROVINCE OF THE MEDITERRANEAN SUBAREA

The combination of West European and Central Asiatic elements is characteristic for the province, but the latter were represented, as a rule, by different species (Vangengeim and Pevzner, 1991).

In Transcaucasia, the Kvabebi fauna with *Anancus arvernensis* and *Hipparion crusafonti* and similar Gomareti fauna are dated as early Villafranchian (Gabuniya, 1986). The Kvabebi fauna is distinctive in its abundance of bovines of the genus *Ioribos* (close to *Leptobos*), as well as wool and horse antelopes (Vekua, 1972). Judging by the evolutionary level of hipparion (Eisenmann and Sondaar, 1989) and by the presence of *Eucladoceros*, this fauna belongs to the second half of the early Villafranchian. The deposits have a normal polarity and are correlated with the second half of the Gauss epoch (Vangengeim and Pevzner, 1991).

UPPER RUSCINIAN–EARLY VILLAFRANCHIAN FAUNAS OF THE EUROPEAN-SIBERIAN SUBAREA

As a whole, the faunas of the subarea were similar in composition to those of West Europe, although differing in the presence of the ochotonids *Ochotonoides* and *Ochotona*, and in the camels of the *Paracamelus* genus. In eastern regions, some European elements (*Dolomys* and *Pliomys*) were absent and some central asiatic forms were distributed. Unlike West European faunas, voles of the genus *Villanyia*, and roe deer of the genus *Capreolus* appeared in that subarea in passing from the Ruscinian to the Villafranchian. Horses of the genus *Equus* may have possibly migrated there as well.

In Romania, the faunas, transitional from the Ruscinian to Villafranchian, are known from the Dacic basin (Malusteni, Ciuperceni 2 localities, and others).

The Malusteni fauna refers to the bottom of the Romanian or is correlative with the Dacian–Romanian boundary; its age is estimated as 3.9 - 4 Ma (Radulesco and Samson, 1989; Radulesco *et al.*, 1989). The vole *Promimomys moldavicus* (= *P. davakosi*), *Hipparion malustense* (similar to *H. crassum* from Perpignan by its evolutionary level), and the large camel *Paracamelus alexejevi* are characteristic of the Malusteni fauna. Together with the typical Ruscinian forms of proboscides, primates, carnivores, and deer, there is also the horse, determined by P. Samson (1975) as *Equus* (*Allohippus*) *major* cf. *exinus*. The presence of the horse in such ancient fauna evokes doubts among many researchers (Eisenmann and Sondaar, 1989). But if the remains of the horse are indeed in the Ruscinian sediments, then obviously the arrival of the horse was due to the land bridge, which existed between Eurasia and America at the end of the Ruscinian. At the same time *Canis* and *Vulpes* came from America, and *Ursus* migrated in the opposite direction (Flynn *et al.*, 1991). Judging by the considerable distribution of animals of open landscapes in the Malusteni fauna, this fauna should be referred to the end of the Ruscinian (the beginning of the global cooling).

The Ciuperceni 2 fauna (3.6 to 3.5 Ma) with *Promimomys occitanus* and *Ochotonoides csarnotanus* may indicate further intensification of the continental conditions (Terzea, 1981).

The Covrigi fauna (Covrigi and Groserea, the Dacic basin; and Iaras-2 and Ilieni, the Brasov depression) is correlated with subzone 16a in Romania (Feru *et al.*, 1983). In composition, the Covrigi fauna hardly differs from the Triversa fauna, but the primitive monodactylous horse, determined as *Equus* cf. *simionescu*, is present in Groserea. The deposits of Iaras-2 have a normal polarity and are correlated with the Gauss epoch not higher than the Kaena episode.

The Cernatesti fauna (Cernatesti and Podari, the Dacic basin) with *Pliomys hungaricus*, *Dolomys milleri*, and primitive elephantine *Archidiskodon rumanus*, coexisting with the Ruscinian species of mastodonts, is referred possibly to the second half of the early Villafranchian. The large horse ex gr. stenonis (*Allohippus major euxinicus*) and small camel *Paracamelus alutensis* are present in the close Tulucesti fauna (Feru *et al.*, 1983). The sediments have a normal polarity and are correlated to the Gauss epoch interval between the Mammoth and Kaena episodes (Feru *et al.*, 1983), but they should possibly be placed in the second half of the Gauss epoch, as the elephant apparently could have appeared on that territory only after 2.9 Ma – when the sea regression began (Haq *et al.*, 1987). As a result of that regression, the basins near the joint of Europe, Asia, and America were considerably reduced, and favorable conditions for faunal changes were created.

On the northern shore of the Black Sea, the top of the Moldavian beds occupies the transitional position between the Ruscinian and Villafranchian. The fauna of the Odessa Catacombs and, possibly, of the lower horizon of the Liventsovka section are of the early Villafranchian age.

The association of the voles with *Pliomys kowalskii* and *Promimomys* ex gr. *stehlini*, typical for the fauna of the Prut river basin (Shevchenko, 1965), allows us to place this fauna on the Kimmerian–Kujalnik boundary, corresponding to that of the Zanclean and Piacenze, or to correlate it with the top of the Kimmerian. The composition of the large mammals resembles the Perpignan fauna, but differs by the presence of *Paracamelus alexejevi*.

The Odessa Catacombs assemblage with a high number of *P. alexejevi* belongs to the beginning of the early Villafranchian, judging by the presence of *Pliomys* ex gr. *kowalskii-hungaricus* (Topachevsky *et al.*, 1987) in the composition of the micromammalian fauna. The carnivora assemblage including *Pachycrocuta pyrenaica*, *Ursus* ex gr. *ruscinensis-minimus*, *Homotherium*, *Megantereon*, and *Chasmaportetes* is close to that of Layna. In M.V. Sotnikova's (1989) opinion, *Chasmaportetes* from the Odessa Catacombs has a more progressive morphotype M_1, than that from Layna. The deposits are reversely magnetized and correspond to the end of the Gilbert epoch (Vangengeim and Pevzner, 1991).

In Bashkirya, the fauna of Simbugino with the beaver *Trogontherium minus*, swamp lemming *Synaptomys mimomyformis*, deer *Eucladoceros*, and others (Sukhov, 1977) can be correlated with the second half of the early Villafranchian.

In the Azov Sea area, the fauna from the lower horizon of the Liventsovka with the dominant species *Mimomys* cf. *hintoni* and *M. reidi* (Topachevsky and Nesin, 1989) seems to be close in age to the subzone MN 16b. V.S. Baigusheva determined *Archidiskodon gromovi*, *Equus livenzovensis*, *Arvernoceros*, and others from the locality, but, unfortunately, it is unknown whether their remains came from the same horizon. The overlying sediments are referred to the middle Villafranchian. The deposits have a reversed polarity and correspond to the beginning of the Matuyama epoch (Vangengeim and Pevzner, 1991).

UPPER RUSCINIAN–EARLY VILLAFRANCHIAN FAUNAS OF THE CENTRAL ASIAN SUBAREA

The ochotonids, jerboas, *Prosiphneus*, and camels were typical for this subarea, which has a rather continental climate. The voles, proboscides, and ungulates were represented by peculiar species, and carnivores by peculiar subspecies. A large number of the Eurosiberian forms were present in faunas inhabiting the transitional zone between Euro-Siberia and Central Asia.

Not less than 14 genera of large mammals appeared during the first half of the early Villafranchian. Besides the genera occurring in other paleozoogeographic provinces of Paleoarctic (*Megantereon*, *Homotherium*, *Lynx*, *Acinonyx*, and *Capreolus*), six new genera (*Postschizotherium*, *Orchonoceros*, *Sinoryx*, *Antilo-*

spira, *Megalovis*, and *Lyrocerus*) appeared in Central Asia. Three genera (*Archidiskodon*, *Canis*, and *Vulpes*) invaded this territory. Forms of genera such as *Talassictis*, *Acerorhinus*, *Paracervulus*, *Platycemas*, *Antilospiroides*, and *Tragoceros* became extinct, and two others (*Metacervulus* and *Eostyloceros*) migrated to regions with a more humid climate. The composition of micromammal assemblages had a fundamental renovation: *Trischizolagus*, *Lophocricetus*, *Cricetodon*, *Microtodon*, and others disappeared, while *Mimomys* and *Villanyia* appeared.

In the early Villafranchian, the hares of the *Alilepus* (*A. annectens*) and *Hypolagus* genera (*H. schreuderi*), ochotonids such as *Proochotona* (*P.* cf. *eximia*), *Ochotonoides* (*O. complicidens*), and *Ochotona* (*O.* cf. *lagreli*), voles *Mimomys youhenicus*, *M. bachiaonicus*, and *M. orientalis* appeared, and those of the genera *Promimomys* (*P. stehlini* and *P. gracilis*) with rootless molars and *Prosiphneus* (*P. praetingi* and *P. paratingi*) became widespread. The early form of *Hipparion houfenense* was replaced by a later one, and *H. sinense* appeared instead of *H. pater* (Qiu *et al.*, 1987). Mastodonts of genera *Zygolophodon* and *Stegodon*, giraffes of the genus *Palaeotragus*, deer of the genus *Cervavitus*, and others still existed. Large deer of the genera *Axis* and *Cervus* replacing early Pliocene muntjaks and antilopes of the *Gazella* (*G. sinensis*) and *Antilospira* genera were widely dispersed.

During the second half of the Early Villafranchian, the rinoceros *Coelodonta* obviously appeared.

By the end of the early Villafranchian, *Parameles* became extinct, *Agriotherium* and *Procapreolus* migrated into South Asia, and *Chasmaportetes* and *Pannonictis* (= *Trigonictis*) migrated into America.

In Kazakhstan, faunas of Ostraya Sopka and Esekartkan are referred to the subzone MN 16a.

Proochotona cf. *eximia*, *Pliomys kowalskii*, *Promimomys gracilis*, *P.* cf. *stehlini*, and *Villanyia praehungaricus* occur in the Ostraya Sopka sequence, situated on the Irtysh river upstream of Semipalatinsk (Bazhanov *et al.*, 1968). The presence of *Meriones*, *Paracamelus praebactrianus*, and *Axis ubensis*, adapted to life on rather dry ground, testifies to relatively arid conditions during the time of the existence of this fauna. The deposits have a normal polarity and seem to correspond to the end of the Gilbert epoch.

The savanna type Esekartkan fauna, known from the Tekesskaya depression of Northern Tien Shan, includes together with the mastodont *Anancus*, the *Hipparion houfenense*, the giraffe *Palaeotragus*, the antilopes *Antilospira*, and the *Gazella sinensis*.

In southern Siberia, the fauna of the Saraiskaya Bay locality, specifically the Ol'hon Island (Baikal), corresponds to the late Ruscinian. Lagomorphs of the genera *Hypolagus* and *Alilepus*, the cricetids *Lophocricetus*, *Microscoptes*, and *Microtodon*, the vole *Promimomys* ex gr. *stehlini*, *Prosiphneus* cf. *ericksoni*, the progressive muntjac *Eostyloceros maci*, and other forms were determined from the Odonims Member (B) of the Sasinskaya Formation of the above locality (Mac *et al.*, 1982). The layers have a normal polarity and are correlated with epoch 5 (Mac *et al.*, 1982), but judging by the evolutionary levels of *Promimomys* and *Eostyloceros* forms, they correspond most likely to the Gilbert epoch. On the whole, the composition of the fauna reflects an intensification of climate aridity, which might have occurred in the intervals 4.7 - 4.3 and 3.8 - 3.5 Ma of the global coolings, as evidenced by the growth of the ice cover in Antarctica (Ciesielski and Weaver, 1983).

In Transbaikalia, faunas of Udunga and Beregovaya are referred to the early Villafranchian.

The Udunga fauna with *Promimomys* cf. *stehlini*, *Mimomys* cf. *minor*, and *Villanyia* cf. *eleonorae* seems to belong to the subzone MN 16a. There were recognized: the mastodont *Zygolophodon*, hyaenid *Pachycrocuta*, machairodontine *Homotherim*, *Hipparion houfenense*, *H. tchicoicum* (Kalmykov, 1989), large cervines *Orchonoceros gromovi* and *Axis shansius*, roe deer *Capreolus* sp. n. – a descendant of *Procapreolus wenzensis* from Wenze I, Poland (MN 15), small elk, possibly an ancestor of the *Libralces gallicus–Alces alces* line, *Antilospira* cf. *zdanskyi*, and others. The diversity and abundance of animals of the forest biotopes (two genera of melines, wolverine, bears, row deer, and elks) are typical of this fauna, inhabiting the humid climatic zones at the end of the first half of the early Villafranchian.

The fauna of Beregovaya differs from that of Udunga by the presence of *Prosiphneus praetingi*, various species of *Mimomys* (*M. minor*, *M. reidi*, and *M. pseudointermedius*), and *Promimomys*. Such species assemblage in addition to the evolutionary level of *Hipparion* cf. *houfenense* (similar to that of *H. crusafonti* from Roccaneyra) (Eisenmann and Sondaar, 1989), allow us to suggest a younger age (MN 16b) for Beregovaya than for Udunga. The high diversity and abundance of inhabitants of open landscapes in the Beregovaya fauna (ochotonids, *Villanyia*, *Chasmaportetes*, *Acinonyx*, puma-like cats, small canids) apparently reflect lanscape-climatic changes in Transbaikalia, which could have occurred at the end of the Gauss epoch.

In Mongolia, the Khirgis–Nur II fauna is correlated with the late Ruscinian. In the Khirgis–Nur Formation (the upper part of the member A) there were encountered: *Ochotonoides*, various cricetids (*Lophocricetus*, *Cricetodon*, *Microtodon*), *Hipparion* cf. *houfenense* (Devyatkin, 1981), muntjacs *Platycemas infans*, and *Paracervulus bidens*, analogous to the forms known from the Ruscinian faunas of China (Vislobokova, 1990). Judging by spore-pollen data, the sediments accumulated during the phase of relative aridity, when "light-coniferous taiga and broad-leaved forests of the steppe-like type were the dominant forest formations, and the steppe occupied the lower forms of the relief" (Devyatkin *et al.*, 1979).

The Shamar fauna (Ikh-Burge butte) on the Orkhon River is referred to the early Villafranchian in Mongolia. The fauna consist of mainly conspecific forms of the Udunga and Beregovaya localities, but differing from these by a higher diversity of micromammals and carnivora assemblages. These are characterized, among small mammals: *Mimomys hintoni – coelodus*, *Allactaga*, *Sinaptomys* (Devyatkin *et al.*, 1979), and among carnivores: the small *Vulpes*, coyote- and jackal-like canids, *Parameles suillus*, *Pannonictis pachygnata*, and *Viretailurus*. There are many species of the open landscape environments in Shamar. Basalts, underlying similar fossiliferous deposits in the Orkhon valley, were dated as 3.1 ± 0.2 Ma old (Devyatkin, 1981). They are reversely magnetized and refer to the Gauss epoch. The qualitatively new stage in the flora evolution is related to the time span of the Shamar fauna: "the formation of nemoral forests disappeared from the vertical zonation and the arid type of its reorganization began" (Devyatkin *et al.*, 1979).

In North China, the Jingle and Gaozhuang faunas in the Yushe Basin (Shanxi province) and those from Red Layers I and II in the Nihewan basin (Hebei province) belong to the Ruscinian. According to evidence from Yushe, a considerable renovation of the fauna took place in the interval 4 - 3.4 Ma: 16 out of 41 genera of the large mammals and about 60% of species appeared on that territory for the first time (Flynn *et al.*, 1991).

The Gaozhuang fauna, approximately correspondent to the zone II of Yushe, is referred to the Gilbert epoch. The last representatives of *Kowalskia* and first ones of *Pliohyaena* (= *Pachycrocuta*) are found in the upper part of the Gaozhuang Formation (the Quilgou Horizon, c.a. 4 Ma) (Flynn *et al.*, 1991).

The discovery of a milk tooth plate of a true elephant in the Jingle locality allow us either to suggest a younger age than was adopted earlier (Qiu *et al.*,1987), or to relate the first migration of elephants into Asia with the end of the early Pliocene.

The fauna from Red Layer I with *Hipparion* cf. *hippiodus* occurs below the erosional surface, the age of which (3.1 Ma) is accepted based on paleomagnetic evidences (Zheng *et al.*, 1991) but may be older, corresponding to the Gilbert epoch (Li and Wang, 1991). A shift toward the colder climatic phase is traced to the end of the time of accumulation of the overlying Red Layer II with *Hipparion houfenense* and more diverse antilope forms (*Sinoryx*, *Gazella*, and *Antilospiroides*): the spore-pollen spectrum there consists mainly of herbaceous elements with a small amount of subtropical ones, but with a large amount of *Abies* and *Picea* pollen in the upper part of the layer (Zheng *et al.*, 1991).

Faunas of the zone MN 16a are represented in the localities of You-he (Snansi province), Daodi of the Nihevan basin (Hebei province), and Mazegou of Yushe.

The primitive voles *Mimomys youhenicus*, *Elephas* (= *Archidiskodon*) *youheensis*, *Hipparion pater* (determined earlier as *H. houfenense*), and other forms are known from the type locality of the You-he fauna on the You River (Weinan province) (Qiu *et al.*, 1987; Xue, 1981). The remains of *Archidiskodon* are found in the Mazegou Formation of the Yushe basin. They are correlated, according to paleomagnetic data, with a part the Gauss epoch in the interval 3.4 - 2.9 Ma (Flynn *et al.*, 1991). In its composition of small mammals, this fauna is similar to the Daodi fauna from the lower part of the Nihowan Formation of Yangyuan and Yuxian, where there are more progressive *Mimomys orientalis*, *Prosiphneus paratingi*, and *Hipparion sinense* (Flynn *et al.*, 1991). The fauna from the lower part of the Nihowan Formation is thought to exist in the interval 3.1 - 2.8 Ma (Li and Wang, 1991). The horizon with small mammals is normally magnetized and correlated with the Gauss epoch just above of the Kaena episode. The age of the horizon is estimated to be within the limits of 2.9 - 2.8 Ma (Li and Wang, 1991).

The Tunliu fauna from the Xicun Formation (Shansi province) with *Mimomys bachiaonicu* resembles the early Villafranchian faunas of Transbaikalia in artiodactyls composition (Zong *et al.*, 1982). In its composition the appearance of the rhinoceros *Coelodonta* gives rise to the thought that it belongs to the second half of the early Villafranchian. The Danangou (Dongyaozitou) fauna of the Nihewan basin with *Zygolophodon* is close to this fauna in age. The animals of open landscapes (*Coelodonta*, camels, antilopes, and others) were widespread during this time in North China. The horse of the genus *Equus* appeared there at approximately 2.5 Ma.

The change in the climatic conditions from humid to arid and the environmental reorganizations occurred during that time in North China. They were caused not only by the global climatic events, but also by orogenic movements (Wu *et al.*, 1991). Mixed coniferous and broad-leaved forests were replaced in this region by steppe vegetation (Lindsay *et al.*, 1980).

CONCLUSION

Thus, we can state that the renewals of the mammalian faunas in the middle latitudes of Eurasia at the end of the early Pliocene and beginning of the late Pliocene were approximately synchronous with the global climatic events, although single phyletic lines did not undergo fundamental changes.

The beginning of the transformation was related to the start of cooling, which caused an increase in aridity. The most remarkable renovations happened under a maximum cooling, when the most thermophilic species disappeared and more cryophilic ones appeared. Only forms with a rather wide tolerance or with a corresponding specialization penetrated the filter of maximum cooling accompanied by complex abiotic and biotic changes. A portion of the less eurythermal and tolerant species could survive on account of their migration into the territories with more favorable climates and environments. Later, they could return to the territory that they previously inhabited with the new waves of migrations.

The largest faunal change occurred at the early-late Pliocene boundary as a result of the cooling in the interval 3.8 - 3.5 Ma. During that time, an important renovation of the generic composition took place because of evolutionary transformations and migrations. Not less than 21 genera of large mammals appeared and not less than six of their genera became extinct in the middle latitudes of Eurasia. The majority of species were autochthonous and a smaller part was represented by immigrants.

The presence of forms typical for the first half of the early Villafranchian, indicates that the fossil-bearing deposits should be referred to the base of the upper Pliocene.

The coolings of 3.2 - 3.1 Ma and 2.6 Ma influenced the evolution of some phyletic lineages mainly at species and subspecies levels. They caused the adaptation of some forms to more arid conditions, and a wider distribution of animals of the open landscapes. An insignificant renewal of the generic composition was caused by immigration from other territories.

A less notable renovation of the fauna was found at the early-middle Villafranchian boundary: not less than four genera of the large mammals appeared and disappeared.

The renewal of the faunas occurred not only because of the evolutionary transformations, but also because of waves of migrations and invasions along the land bridges, which had arisen during the drops in the World ocean level.

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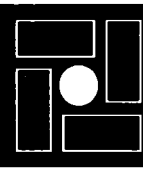

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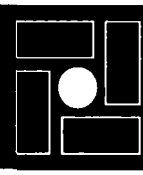

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